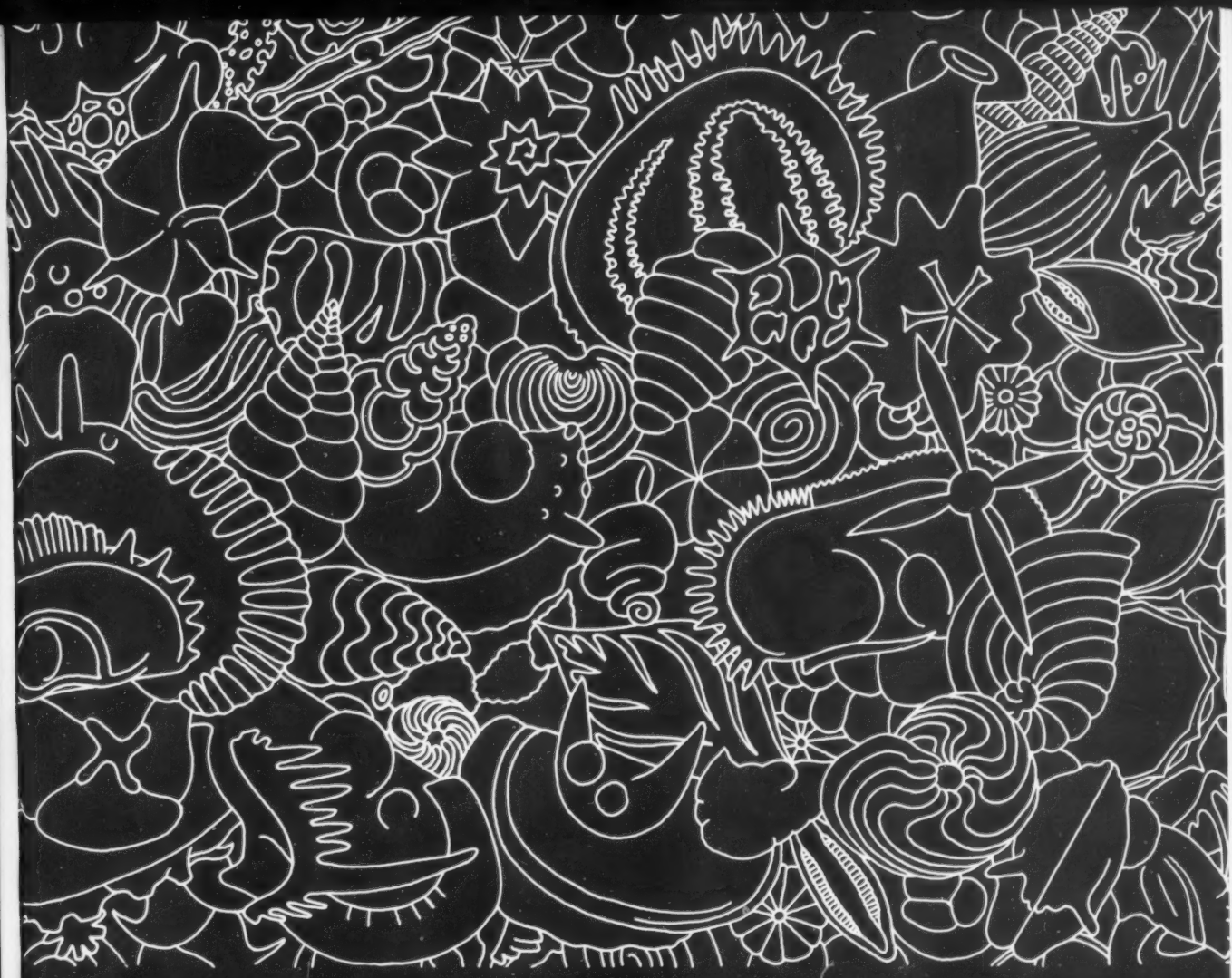

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ABSTRACT

Widespread but seldom-observed morphological features of fossil dinoflagellates and some hystrichospheres relate to the ways in which the test ruptures, and the manner in which the plate pattern of a motile dinoflagellate is reflected on the cyst that formed within it. Evidence is presented that many post-Paleozoic hystrichospheres are dinoflagellate cysts. Criteria for recognizing fossil dinoflagellates and for distinguishing encysted and free-swimming stages are presented and applied to 112 genera variously described as dinoflagellates, hystrichospheres, or incertae sedis. Selected aspects of the morphology of twenty-two described and several undescribed genera are illustrated and discussed.

Observations on the morphology of fossil dinoflagellates

WILLIAM R. EVITT
Jersey Production Research Company
Tulsa, Oklahoma

INTRODUCTION

This paper presents some preliminary results of a study of fossil dinoflagellates and hystrichospheres being carried out at the Jersey Production Research Center in Tulsa. The conclusions to which I have come have important bearing on the recognition, description, and interpretation of the affinites of the fossils studied. Therefore, it seems desirable to set forth my ideas for critical consideration by other workers in the field. Many of the interpretations presented are at variance with, or are marked extensions of, opinoins that have been expressed previously by others. If the discussion suggests answers to some old questions, it also raises new questions that invite further study. My interpretations are based as far as possible on examination of original material; however, they are extended to some described specimens that I have not seen. Certainly, the discussion contains some inaccuracies, for this is a preliminary report incorporating many tentative conclusions of research still in progress. I hope the errors will prove to be minor ones that will soon be corrected. The purpose of this paper will have been served if it provides a fresh insight into the complex relationships of these microfossils and if, in so doing, it inspires more critical observation of the morphological features on which progress in paleontology depends.

Our studies so far show that many previously unrecognized or seldom-reported morphological features, which are useful in distinguishing taxa of dinoflagellates and hystrichospheres, are actually widespread and easy to observe. These features, discussed below and illustrated with selected examples, fall into two general categories. Some of them relate to distinctive ways in which the walls of many of these fossils rupture. Others show how the wall and processes (spines, etc.) of a cyst that formed within a free-swimming (motile) dinoflagellate may reflect the pattern of plate arrangement characteristic of the outer wall. An analysis of the features indicates that many post-Paleozoic hystrichospheres (including such important genera as *Hystrichosphaera*, *Hystrichosphaeridium*, and *Cannosphaeropsis*) are actually cysts of dinoflagellates.

Criteria are listed for recognizing fossil dinoflagellates and for distinguishing encysted from free-swimming stages. Following this, comments are offered on selected genera not already discussed in the main thesis of the paper. In these comments, attention is focused on several major problems and unanswered questions that still confront us. Finally, using the criteria stated earlier, a tentative interpretation of the morphology of most described genera of dinoflagellates, hystrichospheres, and similar types of uncertain position is presented in tabular form.

Acknowledgments

The following persons contributed to the progress of this project by discussing with me the ideas contained in this report or by allowing me to study collections of fossils prepared by them or in their care. I am indebted to them for their many courtesies, and extend my gratitude to: Gerhard Alberti, Geologisches Institut der Stadtuniversität Hamburg, Germany; Trygve Braarud, Biological Institute, University of Olso, Norway; Georges Deflandre, Laboratoire de Micropaléontologie, Ecole Pratique des Hautes Etudes, Paris; Charles Downie, Geological Department, The University,

Sheffield, England; Alfred Eisenack, Geologisch-Paläontologisches Institute der Universität, Tübingen, Germany; Hans Gocht, Wintershall A. G., Barnstorf, Germany; Karl W. Klement, Geologisch-Paläontologisches Institut der Universität, Tübingen, Germany; John J. A. McLaughlin, Haskins Laboratories, New York City; and Ellen Müller, Bentheim, Germany.

Professors Deflandre and Eisenack deserve special mention. The stimulating discussions with each of them and the opportunity to study their extensive collections have been invaluable. They have enthusiastically encouraged me to publish this preliminary account of my interpretations — despite the fact that the views I express are in large measure contrary to those of Professor Eisenack. He has also graciously permitted me to use photomicrographs which I took of specimens in his collection. Professor Deflandre thoughtfully provided a detailed resume of our energetic discussions of the morphology and affinities of dinoflagellates and hystrichospheres, which was of assistance in drafting this paper.

Publication is with the permission of Jersey Production Research Company which has also generously financed publication of the plates.

Terminology and nomenclature

The interpretations suggested in this paper will ultimately require some fundamental changes in the customary terminology and nomenclature of hystrichospheres and dinoflagellates, should they become accepted and are extended by future work. Changes of this sort have been carefully avoided in this preliminary report. Only one new term (archeopyle) is proposed, and no new genera or species are described. In referring to a dinoflagellate or hystrichosphere already described in the literature, the name used in print is cited. In referring to unpublished material, the generic name followed by "sp." is usually used where at least the generic assignment is certain. A number of examples selected to illustrate critical features of morphology are identified simply as sequentially lettered "forms," as *Forma A*, *Formae B* and *D*, etc.

TECHNICAL BACKGROUND

This investigation originated as a study of fossil dinoflagellates. However, the hystrichospheres became inextricably involved. Before new evidence and ideas on the morphology and affinites of these groups are presented, a few remarks are needed on two related subjects: the problem of the hystrichospheres, and the morphology of modern dinoflagellates.

The problem of the hystrichospheres

The possible affinities of the group of microfossils known as hystrichospheres have long puzzled and intrigued those who have studied them. Opinions on the question generally fall into two schools.

One school considers the group polyphyletic, that it includes morphologically similar structures representing a number of different groups of organisms, both plant and animal, such as bryozoans, desmids, crustaceans, and flagellates. According to this school some hystrichospheres are eggs, some are cysts, and others are tests of adult organisms. They are brought together by a similarity in external morphology that has nothing to do with close genetic relationships. At different times during their long geologic history (Precambrian to Recent), different groups may have been the dominant contributors to the fossil record of hystrichospheres, but probably at all times more than one group was represented. Eventually it may be possible to identify some of the groups, but others will probably always remain uncertain because of the lack of sufficiently diagnostic characteristics.

The other school holds that the group is monophyletic, that the similar morphologies of many of the forms referred to it reflect true genetic relationship. This school claims that evolutionary changes have occurred during the long history of the group, but that, on the whole, the hystrichospheres are a unified group of related organisms.

Deflandre (1947) has presented the most comprehensive summary of the problem and the evidence bearing on it. He believes the hystrichospheres are polyphyletic. Eisenack (1954) champions their interrelationship and presents the case for monophyletic origin.

Maier (1959) summarizes earlier work on the chemical composition of hystrichospheres and presents some new data. She notes that a fine-scale intermixture of organic and inorganic materials is evidenced by the fact that some specimens retain their original form (including the finest details) whether they are treated with hydrofluoric acid or heated in a glow-tube. From a study of luminescence phenomena in ultraviolet light, Maier concludes that dinoflagellates and hystrichospheres represent distinctly different groups of organisms and that hystrichospheres belong to the animal, rather than to the plant kingdom. Although photoluminescence may provide clues to the composition of microfossils by revealing hitherto unknown physical properties, the evidence that Maier cites in this instance does not appear to justify at all the conclusions she reaches.

This paper points out specific morphological grounds for identifying some of the hystrichospheres as dinoflagellates. However, this in no way implies that all hystrichospheres were dinoflagellates. I interpret the new evidence to be in strong support of a polyphyletic origin of the hystrichospheres, believing that diverse organic groups, in most cases still unidentified, are also represented.

Morphology of modern dinoflagellates

Remarks about modern dinoflagellates will be kept to a minimum. For more detail the reader is referred to such works as those by Chatton (1952), Lebour (1925), and Graham (1951).

In the motile stage, a modern dinoflagellate (text-figs. 1–4) is propelled through the water by two flagella. In all but the most primitive forms, one flagellum is transverse and more or less encircles the cell, usually in an equatorial position. The other is longitudinal and trails behind. In the thecate dinoflagellates (i.e., those that possess a resistant external covering, or theca) the positions of the flagella are frequently indicated by furrows; the transverse furrow, or *girdle*, and the *longitudinal furrow*. The longitudinal furrow is often a part of a larger circumscribed area, called the *ventral area*. The face with the longitudinal furrow is considered ventral, the opposite surface dorsal. The *apex* of the theca is the end in the direction of forward movement (anterior). The opposite end is the *antapex*. Right and left are used in the conventional manner. The theca is divided by the girdle into an apical part, the *epitheca*, and an antapical part, the *hypotheca*. The apex is frequently extended into a single *apical horn* or point and the antapex into two *antapical horns* or points. Although a basic bilateral symmetry is often apparent, it is rarely, if ever, perfect, and may be quite inconspicuous.

The wall of the theca is commonly divided into a number of polygonal areas, termed *plates*. The number and arrangement of these plates constitute the *tabulation*, which is a feature of taxonomic importance. The plates occur in definite series, more or less latitudinal with respect to the girdle that commonly forms the equator of the cell. The names of the series of plates and the symbols for specifying individual plates are presented in text-figs. 1–4. A tabulate theca of the type described here is characteristic of one large group of modern dinoflagellates. This is the group most abundantly represented in the fossil record. Other types of wall structure occur in both Recent and fossil specimens, but need not receive attention here.

The theca of most Recent and fossil dinoflagellates is chiefly organic in composition. Cellulose seems to be the principal original ingredient, but this is more or less altered in fossil specimens. A noticeable amount of silica may also be present. Fossil types with exclusively calcareous or exclusively siliceous thecae also have been described. However, these are rare and are not considered in this report. For discussions on composition see: Deflandre (1933, 1938*a*, 1938*b*, 1940, and 1952), Eisenack (1936, 1939), and Lefevre (1933).

Almost all modern dinoflagellates appear to reproduce exclusively by binary fission. The immediate products of this fission may be either free-swimming zoospores or daughter cells that are minute replicas of the adult. The fission may occur within the parent theca, or the protoplasm may first leave the theca. Division may take place without obvious preliminary changes, or the protoplasm may first become enclosed in a special, toughwalled structure, the cyst. A resting cyst, unrelated to the reproductive cycle, may form as a purely protective structure in response to unfavorable conditions. To release the products of the reproductive cycle (cyst or free-swimming zoospores), or to release a resting cyst, the theca commonly ruptures, usually along the girdle. The rupture may also occur along a specific series of plate boundaries at an angle to the girdle (e.g., *Ceratium*). Subsequently the two parts of the parent theca may be cast off and abandoned, or they may be incorporated in the thecae of the new daughter cells. The wall of the cyst must also rupture when it germinates. Although cysts have been observed in many Recent dinoflagellates, the exact method of cyst formation and the manner in which the cyst wall ruptures have not been carefully observed. These matters have an important bearing on the study of fossil dinoflagellates, but data on the life cycles and detailed morphology of modern forms are meager. Extensive studies on life cycles of dinoflagellates grown in artificial cultures are now under way at the Haskins Laboratories in New York City. The results of these studies should help us to better interpret the fossil record.

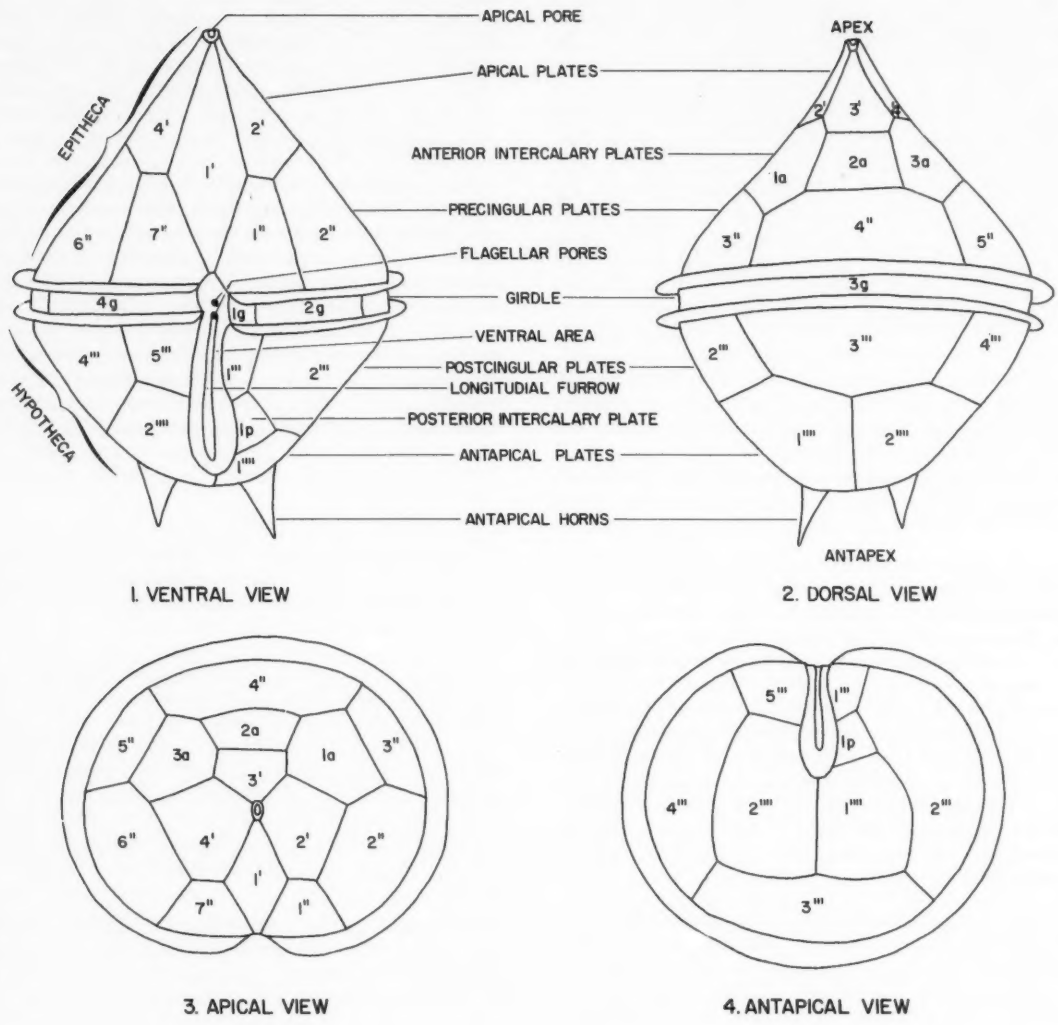
FOSSIL DINOFLAGELLATES

Morphology of motile and encysted stages

The reader is referred to papers by Deflandre (1952) and Eisenack (1958*b*) for general discussions of fossil dinoflagellates. Only the points essential to the present discussion will be presented here.

The same basic thecal structures that are known in modern dinoflagellates occur in fossil ones. In most cases, however, plate patterns of fossil and Recent dinoflagellates are different. Only one modern thecate genus is widely represented among fossils. This is *Gonyaulax*, a genus recognized by its characteristic tabulation, which has changed very little during evolution. It is one of the geologically oldest dinoflagellates as well as one of the most important living thecate genera.

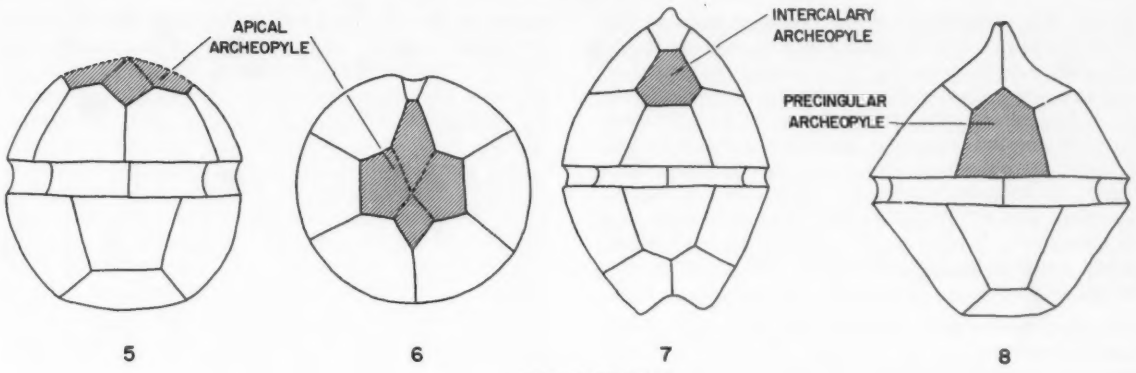
Cysts within fossil dinoflagellates are well known. In some genera the cyst is virtually ever-present, to the extent that it is a useful taxonomic criterion. Eisenack has even suggested that the omnipresence of the cyst in those species of *Deflandrea* studied by him implies that it is not a true cyst (i.e., a relatively transitory structure), but a permanent and more fundamental morphological feature. I believe his argument is fallacious for two reasons. First, with specific regard to *Deflandrea* (pl. 1, figs. 1–4; pl. 2, figs. 1–4), the cyst is not always present. In some populations many individuals (up to 15%) contain no cyst at all, while an equal number show cysts in various stages of development. Whenever present, the cyst is sometimes ruptured, sometimes without any opening. I see no reason to interpret this structure as other than a true cyst. Second, studies on Recent dinoflagellates have shown that encystment can take place very rapidly upon the onset of unfavorable conditions. Since all fossils represent dead organisms, and since death may be assumed to result from "unfavorable" conditions, whatever their exact nature, we should not be surprised to find some species always represented by encysted stages.



TEXT-FIGURES 1–4
DINOFLAGELLATE TERMINOLOGY AND TABULATION

Diagrams of a hypothetical thecate dinoflagellate illustrating the terminology for the principal thecal structures and the symbols used to identify individual plates. The complete tabulation of this example can be described in an abbreviated fashion as follows: 4′, 3a, 7″, 4g, 5‴, 1p, 2⁗, meaning that the theca is composed of four apical plates, three anterior intercalary plates, seven precingular plates, four girdle plates, five postcingular plates, one posterior intercalary plate, and two antapical plates.

Here it is appropriate to stress a fundamental point with regard to the occurrence of cysts in the fossil record: If some species are represented only be cysts, it may merely mean that the non-encysted stage was too delicate to be preserved. It is important to remember that the fossil record normally contains only the relatively more resistant structures. Since many dinoflagellates today have such resistant structures only in the encysted stage, it is likely that this was also true in the past. Therefore, we should expect to find fossil cysts whose motile counterparts were never preserved. An appreciation of this probability is important for an understanding of the later discussion in which many hystrichospheres are interpreted as isolated dinoflagellate cysts free of any trace of originally surrounding cell wall or theca.



TEXT-FIGURES 5–8
TYPES OF ARCHEOPYLE

Diagrams to show the three types of archeopyle formed by release of specific plates from the theca of a motile dinoflagellate (or by release of the equivalents of these plates in the reflected tabulation of dinoflagellate cysts).

5–6 Apical archeopyle, formed by loss of entire apical series of plates (four plates in illustrated example). Sutures between original plates are indicated by dashed lines.

7 Intercalary archeopyle, formed by loss of mid-dorsal anterior intercalary plate.

8 Precingular archeopyle, formed by loss of mid-dorsal precingular plate.

Rupture of the theca

Many fossil dinoflagellates, like the Recent ones, apparently broke open at times to release their contents. The openings that were produced have been mentioned in the literature, but they seem both more widespread and more significant than recognized heretofore. Openings are not known in all fossil forms, however. Some either did not rupture, or we have not yet observed their ruptured thecae. When openings did form, they developed in one of three ways: 1) rupture along the girdle; 2) rupture along the line of sutures between the apical and precingular series of plates; or 3) rupture by release of a single plate of the epitheca, either a precingular plate or an intercalary plate between the apical and precingular series.

Rupture along the girdle divides the theca into more or less equal parts, the epitheca and hypotheca. However, when fossil specimens are found as isolated epithecae or hypothecae, it may be difficult or impossible to determine whether the separation is accidental or not. The girdle is a structurally weak zone in many dinoflagellates. Therefore, rupture along this line may result from mechanical deformation unrelated to the life processes of the organism. In contrast, openings in the epitheca that are regular in shape, correspond to a specific plate or group of plates, and occur repeatedly in specimens from different samples are not likely to be accidental. I believe they have considerable taxonomic significance. Credit goes to Gocht (1959) for first pointing this out in discussing *Cyclonephelium* and *Tenua*, two genera then considered unrelated to dinoflagellates, but interpreted below as dinoflagellate cysts.

To aid in describing the structures resulting from rupture along definite, pre-formed lines, the term *archeopyle* is here introduced with the following definition: the opening in a fossil dinoflagellate (either its motile or encysted stage) formed by the release of a single plate or group of plates. I express my gratitude to G. Deflandre for suggesting the term (personal communication), which refers to the presence of this opening (pyle- gate, orifice) in fossil (archeo-ancient) dinoflagellates; it has not been observed in Recent motile dinoflagellates but is typically developed in some Recent hystrichospheres (genus *Hystrichosphaera*) that I have seen from bottom samples of the Gulf of Batabano, Cuba, and the Gulf of California.

Eisenack's term "Schlüpfolch," although descriptive, has no satisfactory equivalent in French or English, whereas archeopyle, a term without connotation as to function, would be the same in all three languages. The term "pylome" has also been used for these openings (e.g., by Eisenack, and Klement). This term was first used in reference to the more or less circular openings that Eisenack observed in certain Paleozoic hystrichospheres. In this report the term is restricted to openings of that type. A pylome bears no relationship to a dinoflagellate-like system of plates or platelike areas, whereas an archeopyle directly reflects such areas. Therefore, archeopyle is applicable only to dinoflagellates, whether motile stages or hystrichosphaeroid cysts.

Rupture along the line between the apical and precingular series of plates releases the apical plate or the group of apical plates to form an opening at the pole. This is an *apical archeopyle* (text-figs. 5, 6). Rupture by

release of a single plate of the epitheca leads to the formation of two other distinct types of archeopyle. An *intercalary archeopyle* (text-fig. 7) is formed by release of an intercalary plate and a *precingular archeopyle* (text-fig. 8) by a plate of the precingular series. In both cases the plate released occupies a mid-dorsal position and is, in itself, conspicuously bilaterally symmetrical. The apical archeopyle characteristically has a zigzag boundary that reflects the angular plates along the line of separation. Similarly, the precingular and intercalary archeopyles typically reflect the shape of the individual plates.

It is worth noting that, although the archeopyle essentially corresponds to a specific plate or group of plates, the separation that forms it does not take place exactly along the plate boundaries (Klement, 1960). Rather, the separation develops parallel to the suture, but a short distance from it on the plate or plates that are being released (pl. 1, fig. 5; pl. 2, fig. 5). The same type of separation has also been observed in some fossil forms that divide along the girdle, suggesting that the large opening formed in them by loss of almost the entire epitheca can be considered a fourth type of archeopyle. An example of this is *Gonyaulax ornata* (Klement, 1960), in which the division line runs parallel to the girdle across the lower ends of the precingular plates, leaving the entire girdle and a narrow band from these plates on the separated hypotheca. A second example is shown by pl. 1, figs. 6, 7, and 9, and a third by Eisenack and Cookson's (1960) excellent photomicrographs of *Oodnadattia tuberculata*. When we know more about rupture in the girdle region, perhaps recognition of this large variety of archeopyle will be desirable. For the present, however, it seems advisable to restrict the term to the smaller apical, intercalary, and precingular openings, which can be more readily distinguished from accidental breaks than can separations in the theca that occur along the girdle.

Rupture of the type that produces an archeopyle as defined above has not been observed in modern dinoflagellates. Conversely, separation of the theca along an oblique line (as in Recent *Ceratium*) is as yet unknown among fossils. Nor do known fossils show an opening like the one that also forms in *Ceratium* by loss of the plates of the ventral area, or the type that occurs in certain *Gonyaulax* and *Spiraulax* (Kofoid, 1911) by opening of several of the sutures between the apical plates.

Except for the distinction made between the two different plates involved in formation of the intercalary and precingular archeopyle, these observations are not new. We do not know the significance of the differences among the several types of rupture known to occur. Some genera seem to be characterized by one type only; others are not. Fossil *Gonyaulax* shows two types: a precingular archeopyle and a separation along the girdle; in Recent *Gonyaulax*, opening of the sutures between the apical plates is common. Perhaps different types of rupture were associated with release of zoospores on the one hand and release of a larger mass of protoplasm on the other. In light of the known life history of modern dinoflagellates, it seems logical to interpret the openings in fossil representatives as exits for protoplasm, either in the form of resting or reproductive cysts, or as zoospores. Several authors have noted these possibilities (e.g., Deflandre, Eisenack, Klement, Gocht). However, a species of *Deflandrea* soon to be described shows that this was not always the sole function of the opening. In this species the opening (an intercalary archeopyle) occurs in specimens that contain a fully formed but unruptured cyst (pl. 1, fig. 4; pl. 2, figs. 3–4). Therefore, the opening must have had some purpose other than serving as an exit for the contents of the cyst. However, the opening may later have served as such an exit in those specimens whose cysts are ruptured.

EXAMPLES OF FOSSIL DINOFLAGELLATES

Let us now turn to a consideration of several examples of fossil specimens and the information that they provide.

Gonyaulax

Plate 1, fig. 5, and pl. 2, fig. 5, clearly show the precingular archeopyle that occurs in most fossil specimens of this important modern genus. Many authors have called attention to this structure. The small plate released in forming the archeopyle in this genus is occasionally found separately (pl. 1, fig. 8). The illustrations show that the rupture line that frees the cover of the archeopyle runs a short distance from the plate boundary, leaving a narrow strip of the plate 3″ to form the margin of the archeopyle. As already noted, the same feature is shown by specimens that rupture along the girdle (pl. 1, figs. 6, 7, 9).

Lithodinia and Formae A and B

Lithodinia jurassica Eisenack, 1935 (pl. 1, figs. 10–13; pl. 2, fig. 6), is a small species of compact form that shows the typical structures of a thecate dinoflagellate: well-developed plates, girdle, and ventral area. An apical archeopyle is usually present, although in some specimens the apical plates are still in place. The archeopyle margin is zigzag, with the most prominent notch where plate 1′ extends a greater distance toward the girdle than the other apical plates.

Forma A (pl. 1, fig. 14; pl. 2, fig. 7) differs from *Lithodinia* in tabulation, but shows a very similar archeopyle. The plate boundaries are unusually clear. *Forma B* (pl. 1, figs. 15–17; pl. 2, fig. 8) differs from *Forma A* only in details that are not pertinent to this discussion.

The tabulation of all three of these types agrees with that of *Gonyaulax*, and Eisenack has recently stated (personal communication) that he now believes *Lithodinia jurassica* should be referred to *Gonyaulax*. However, I feel that the difference in type of archeopyle should be more fully evaluated as a generic criterion before assigning these three forms to *Gonyaulax*.

Formae C, D, and E

In contrast to the preceding three examples, *Forma C* (pl. 1, fig. 18; pl. 2, fig. 9), is a fossil that cannot readily be interpreted as a motile dinoflagellate, since it lacks all indications of a functional girdle or longitudinal furrow. In fact, unruptured specimens show almost no suggestion of dinoflagellate affinity. However, ruptured specimens show certain important similarities to *Lithodinia* and *Formae A* and *B*: the rupture line has an irregular zigzag course, with short clefts extending from the re-entrant angles. This clearly defined margin suggests a latitudinal series of polygonal areas around the opening. In addition, the deepest notch in the margin resembles the notch that marks the position of the ventral furrow in *Lithodinia* and *Formae A* and *B*. In short, the opening appears to be an apical archeopyle whose limits reflect a dinoflagellate-like tabulation.

Many variations on this theme occur (for example, pl. 1, figs. 19–21; pl. 2, figs. 10–12; pl. 3, figs. 1–4), but the features associated with the rupture line are strikingly constant. It is the shape and surface ornament that are variable. For example, the surface opposite the opening may have a smoothly rounded or decidedly invaginate outline, and the surface ornament (shown in the photomicrographs, but omitted from the drawings) varies between wide extremes. The ornamental elements may be distributed without recognizable pattern, aligned in rows (which reinforce the impression of a dinoflagellate-like tabulation), or limited to the marginal area, leaving bare a central region on one or both sides. Few fossils of this general type have been described in the literature. However, the genera *Tenua* (pl. 1, fig. 22; pl. 5, fig. 1) and *Cyclonephelium* (pl. 5, fig. 2) that Eisenack (1958*a*) and Deflandre and Cookson (1955), respectively, described as hystrichospheres, have this type of morphology.

An explanation of the morphology of *Forma C* and of its similarity to that of fossils like *Lithodinia* and *Formae A* and *B* is suggested by *Formae D* and *E*. *Forma D* (pl. 3, fig. 5; pl. 5, fig. 5) is a species similar to the one described as *Ceratocystidiopsis ludbrooki* (Cookson and Eisenack, 1958; Cookson, 1960). It has a thin outer wall with the typical form of a motile dinoflagellate. Prominent apical and antapical horns are present. The tabulation is obscure in all specimens, but a girdle is indicated in some. Inside, a thicker-walled structure occurs on which apical and antapical convexities suggest very much abbreviated horns; no girdle is visible on the inner structure. Close examination shows that both inner and outer walls are ruptured along a zigzag line running around the specimen between the girdle and the apical pole. Separated specimens (pl. 3, fig. 6; pl. 5, figs. 3–4) are more common than whole individuals. Specimens of the inner structure that retain only vestiges of the thin outer wall are occasionally found (pl. 3, fig. 8).

Forma E (pl. 3, figs. 9–14; pl. 5, fig. 7) is a dinoflagellate whose basic structure recalls *Forma D*, with a denser structure inside a thin outer wall. However, greater detail, visible in well-preserved and advantageously oriented specimens, is especially instructive: The outer theca is clearly tabulated and the sutures between the plates are marked by low lamellae extended into delicate, flexible, spinelike projections. The wall of the inner structure, on the other hand, bears granules of varied size. The larger ones are in rows that define polygonal areas separated by narrow zones devoid of ornament. Like *Forma D*, both inner and outer walls rupture along the zigzag line between the precingular and apical plates, thus forming an apical archeopyle.

Cysts and reflected tabulation

My conclusions from the data and observations presented up to this point are as follows:

1) The inner bodies in *Formae D* and *E*, and the fossils here grouped as *Forma C*, are dinoflagellate cysts.

2) The cysts of some fossil dinoflagellates (e.g., *Formae C* to *E*) ruptured to form an apical archeopyle similar to that in *Lithodinia*.

3) The cysts of some fossils dinoflagellates (e.g., *Formae C* to *E*) exhibit features that reflect the tabulation of the theca. These may be elements of surface ornament (ridges or rows of spines or granules) or lines of rupture in the wall. The reflections of tabulation tend to be most conspicuous along the line of rupture.

4) In some species the cyst and theca remain fixed to one another; in others isolated cysts occur both in ruptured and unruptured states. The isolated cysts may represent species with non-thecate motile stages. Alternatively, their thecate motile counterparts may be represented by other types of specimens in the same assemblages.

Hystrichosphaeridium

From this point in the discussion we may wander farther afield and look at some fossils that more definitely have the morphology of hystrichospheres than the cysts described above. First, let us take the genus *Hystrichosphaeridium*, one of the longest recognized and most "typical" of all hystrichospheres. An array of specimens representing several species of the genus are illustrated (pl. 3, figs. 15–19; pl. 4, figs. 1–6, 9–10; pl. 5, figs. 8–12). *H. recurvatum* is a member of the "tubiferum group" (Lejeune-Carpentier, 1939), so called for the type species of the genus, *H. tubiferum* (Ehrenberg). Consideration of these illustrations will show the following:

The processes are systematically arranged with respect to a polar opening formed by rupture along a zigzag line (pl. 4, figs. 1–4, 10; pl. 5, fig. 8). The rupture, in conjunction with short branches from it, partly delimits four plates forming the polar cap (pl. 3, figs. 15–16; pl. 4, fig. 2; pl. 5, figs. 11–12) and six (or seven) plates on the main body along the opening (pl. 3, fig. 16; pl. 5, fig. 8). Usually a single process rises from the

center of each plate thus defined. One or two of the processes on the main body along the opening may be somewhat smaller than the rest (pl. 4, fig. 10). At the other pole, a polar process and a latitudinal row of processes some distance from the pole can be recognized (pl. 4, fig. 5), but no indication of plate boundaries can be seen. A cluster of small, irregularly arranged processes, which includes as its terminal members the one or two smallest processes along the margin of the opening, may occupy a meridionally elongate area on the main body (pl. 4, figs. 9–10). A more or less equatorial belt is marked by a row of processes structurally like the rest (pl. 4, figs. 2–3; pl. 5, fig. 8), by a row of processes quite different from the rest (pl. 4, fig. 5), or by a zone without any processes at all (pl. 4, fig. 6). This equatorial belt is interrupted by the cluster of small processes when they are present. In some cases the processes are hollow with flared tips (pl. 3, fig. 16; pl. 4, figs. 2, 5). In others the shaft wall is incomplete, being composed of somewhat anastomosing strands, and the flared tips are conspicuously polygonal, suggesting a series of platelike structures external to the processes themselves (pl. 3, figs. 17–18; pl. 5, figs. 9–10).

The correlation of these features with ones already discussed in the preceding examples of motile dinoflagellates and dinoflagellate cysts is striking. I interpret *Hystrichosphaeridium* as a dinoflagellate cyst with an apical archeopyle, in which both rupture lines and processes reflect a conventional tabulation of an original outer wall that has not been preserved. The actual physical relationship of the processes to that original outer wall also deserves discussion, but this is better deferred until later.

Observation of platelike structures in *Hystrichosphaeridium* is not new, although they have seldom been mentioned in the literature. Lejeune-Carpentier (1939) observed them in *H. tubiferum* and its allies and figured a group of four plates (pl. 5, fig. 12), which I consider to be the apical series released in formation of the archeopyle. Deflandre (1937) earlier had noted and figured plate boundaries in *H. horridum*. Re-examination of the type specimen of *H. horridum* suggests that the visible plate boundaries are actually the separation line along the margin of the archeopyle whose cover is cracked open in this specimen but not displaced. The dark coloration and the orientation of the specimen prevent absolute certainty on this point.

Hystrichosphaera

Let us now turn to another "typical" hystrichosphere: *Hystrichosphaera* Ehrenberg, the type genus of the family Hystrichosphaeridae and root of the informal terms hystrichosphaerid and hystrichosphere. The dinoflagellate-like characteristics of *Hystrichosphaera* already have been adequately described and discussed, for example by Deflandre (1947), Lejeune (1937), and Eisenack (1954). Little need be repeated here. A distinct, spiral girdle-like structure and a surface divided into conspicuous polygonal areas suggesting plates are well known. Ridges mark the boundaries between polygonal areas, and spinelike processes, characteristically branched at their tips, rise from the intersections of these ridges. The polygonal areas are grouped to suggest the plate series of epitheca, girdle, hypotheca, and ventral area in a typical dinoflagellate. Nevertheless, as Eisenack (1954) has ably pointed out, *Hystrichosphaera* is no "normal" dinoflagellate. First, the girdle is not a functional girdle capable of receiving a flagellum, for it is often crossed by relatively high membranes rising from the ridges that divide it into elongate polygonal areas. Second, the platelike areas are not true plates in the typical dinoflagellate sense in that they are not separable along bounding sutures. Third, the girdle-like band is often of unusual design, not parallel-sided with quadrangular constituent elements as in a motile thecate dinoflagellate, but with zigzag boundaries along its elongate hexagonal elements. These are conditions unknown in motile dinoflagellates.

Illustrated here (pl. 4, figs. 14–16; pl. 5, figs. 13–14) is a species of *Hystrichosphaera* with relatively simple morphology in which the characteristic features of the genus are easily seen. In many species the elaborate and prolific processes may make it difficult to work out the tabulation in detail. Unlike *Hystrichosphaeridium*, *Hystrichosphaera* has a precingular archeopyle, whose frequent occurrence and constant position on the dorsal surface have often been noted. The archeopyle resembles that in *Gonyaulax*.

Klumpp (1953, p. 387) reported having seen a *Hystrichosphaera* in which the tabulate and process-bearing test was only a thin veil about a darker, inner cyst of uncharacteristic form. She accepted this as proof that hystrichospheres were independent organisms (i.e., not cysts) that formed cysts either regularly or in response to unfavorable circumstances. I do not believe her conclusion necessarily follows from the evidence, and would speculate that in this exceptional case a second cyst formed within the hystrichosphere which was already a cyst. Perhaps this occurred because the first cyst was imperfectly formed, as evidenced by its delicacy. Unfortunately, the specimen in question was damaged during study and no similar observations have been reported since.

Attempts to interpret *Hystrichosphaera* as a dinoflagellate have been futile, for it seems to be a structure incapable of functioning as a motile form. However, I suggest that *Hystrichosphaera* is a dinoflagellate cyst whose features, like those of *Hystrichosphaeridium*, are inexact reflections of the features of a motile dinoflagellate.

Forma F

We can now consider the origin of the characteristic processes in both *Hystrichosphaeridium* and *Hystrichosphaera*, and their relationship to the original outer wall of the dinoflagellate. For this, an examination of the morphology of *Forma F* is particularly instructive. *Forma F* (pl. 6, figs. 1–5; pl. 7 figs. 1–2) consists of an

elliptical wall with a spiral shelflike flange around the equator. A large complex process lies at each pole. Four smaller processes are regularly arranged in a latitudinal zone between each pole and the equator. A group of still smaller processes lies in part between the two offset ends of the equatorial spiral, and short spinelike projections are scattered over the surface. On the surface opposite the gap in the equatorial band there is an opening like the precingular archeopyle in *Gonyaulax* and *Hystrichosphaera*.

It is clear that *Forma F*, like *Hystrichosphaera*, has certain dinoflagellate-like features. It is also clear that the equatorial structure (even more certainly than the one in *Hystrichosphaera*) was not a functional girdle, and that no longitudinal furrow was present. How, then, are we to interpret these structures? Close examination shows that the distal tips of the processes have a significant structure and position. The tips are slightly flared—those of the polar and equatorial processes more or less symmetrically, those of intermediate ones obliquely. The polar processes are much longer than the equatorial ones. Ones at intermediate latitudes are of intermediate length. The whole configuration (pl. 7, figs. 2) suggests that the tips of the processes were formed against the inner surface of an enclosing ellipsoidal wall. In other words, the solid wall we now see is a cyst, formed within a (presumably) thin-walled cell and more or less centered within that cell by the processes that now rise from the inner wall. All trace of the outer wall has been destroyed.

A number of other genera provide more direct evidence that processes of a variety of types, such as occur in hystrichospheres, actually developed as supports between the cyst and the theca of encysting dinoflagellates. In *Forma D*, such processes are seldom seen, but when they do occur (pl. 3, figs. 6–7; pl. 5, figs. 3, 6) their origin is fairly obvious. Similar structures are abundant in *Chlamydophorella* and *Scriniodinium trabeculosum* (pl. 7, fig. 9). Numerous well-developed supports, but with only occasional fragments of the outer wall, are present in *Aptea polymorpha* (pl. 8, fig. 18). In *Triblastula* (pl. 6, fig. 7; pl. 7, fig. 5), whose general shape and polar structures strongly suggest dinoflagellate affinities, the central cyst is joined to the polar surfaces by similar supports. The morphologically simple variant of the *Cannosphaerospsis*-like species shown in pl. 4, fig. 3, shows a tenuous remnant of the outer wall stretched over the large polygonal plate area in the hypotheca that is outlined by supports rising from the cyst proper. These genera are discussed later.

Origin of processes

I interpret the processes of *Hystrichosphaeridium* and *Hystrichosphaera* in the same way; that is, as structures that braced the cyst against a now-missing outer wall. The flattened or flared tips of the processes in *Hystrichosphaeridium*, and the short branches at large angles to the shaft in *Hystrichosphaera*, originally lay against the inner surface of this wall. In *Hystrichosphaeridium*, the polygonal tips of the processes are a direct reflection of a primary tabulation of the outer wall. In both *Hystrichosphaeridium* and *Hystrichosphaera*, the polygonal areas on the wall of the cyst itself are less direct reflections of this tabulation. In *Hystrichosphaeridium*, the tabulation reflected on the cyst becomes apparent only when the cyst ruptures and an archeopyle is formed, but in *Hystrichosphaera* the tabulation is distinct on the unruptured cyst. In *Hystrichosphaera*, a precingular archeopyle of the *Gonyaulax* type occurs.

This interpretation explains both the similarity and difference between typical hystrichospheres (like *Hystrichosphaeridium* and *Hystrichosphaera*) and typical motile dinoflagellates. The objections to considering *Hystrichosphaera* a dinoflagellate disappear if one considers it a dinoflagellate cyst whose features simulate, replicate, or abbreviate the typical morphology of a motile dinoflagellate in the same way that the markings on the cyst in *Formae D* and *E* reflect the features of the outer thecae in those more obvious dinoflagellates.

CRITERIA FOR INTERPRETATION

In interpreting fossil specimens on the basis of the preceding discussion two related questions of importance arise: 1) By what specific criteria can a hystrichosphere that is a dinoflagellate cyst be distinguished from one that is not? 2) How can a dinoflagellate cyst be distinguished from a motile stage? The first question is the more important since it concerns recognition of the major group of organisms to which a fossil belongs. The second question is less important. Both questions deal with the establishment of limits between groups of natural objects. Since boundaries in nature are seldom sharp, it is not surprising that the criteria listed below, although effective in many cases, will not work in all. They are the best that can be formulated at the moment, but we expect alterations and refinements as we learn more about the morphology of the fossils involved.

In answering the first question, the criteria that seem to be most useful in recognizing a hystrichosphere as a dinoflagellate cyst are a follows:

1) Subdivision of all or part of the wall into polygonal areas suggesting the plates of epitheca, girdle, and hypotheca of thecate dinoflagellates. These areas constitute a "reflected" tabulation. They may be defined by either surface structures (ornament, processes) or rupture lines.

2) Presence of a particular type of opening, the archeopyle, formed by the release of a portion of the wall corresponding in position and shape to a single precingular or anterior intercalary plate, or to one or a group of apical plates. This is also an expression of the reflected tabulation.

3) Presence of polar or equatorial structures or processes, either dorsal or ventral, that suggest basic elements conspicuous in many dinoflagellates; for example, girdle, ventral area, apical and antapical horns, dorsoventral flattening.

4) Basic bilateral rather than radial symmetry. The symmetry may be imperfect because of a spiral girdle with offset ends, or differences in tabulation or outline.

The shape of the archeopyle is usually highly distinctive. The apical one is generally circular or oval with a conspicuously zigzag margin, whereas the intercalary and precingular ones have a markedly bilateral symmetry. I would consider the archeopyle in itself to be a reasonably reliable criterion of dinoflagellate affinities as long as it reveals its distinctive shape. However, there seems to have been an evolutionary trend, perhaps often repeated in different lineages, toward modification in the shape of the archeopyle from polygonal to round. When this change takes place in a form with other dinoflagellate-like features; it can easily be interpreted. However, if the change occurs in a form lacking such accessory features, recognition as a dinoflagellate cannot be made by application of the criteria discussed above. Instead, recognition must rest on other grounds involving the more subjective judgment and experience of the paleontologist. Probably the best procedure in most such cases would be to consider the types non-dinoflagellates. However, this is not always reasonable. For example, *Hystrichosphaeridium inodes gracilis* Eisenack (1954) is a form with a virtually circular archeopyle and processes positioned without readily recognizable pattern. No girdle is apparent. Yet, it does not seem reasonable to me to dissociate this species from other *Hystrichosphaeridium* with which it shows strong similarity in structure of the processes. I have seen other hystrichospheres, especially in the Late Cretaceous and Early Tertiary, that neatly bridge the gap between forms identifiable as dinoflagellates by the above criteria and ones that are not. In the former, a circular archeopyle is associated with a row of distinctively sized or shaped girdle processes; in the latter, all the processes are alike.

Cases like those mentioned in the preceding paragraph are better settled on an individual basis, rather than by blind application of limited and untested criteria, until our collective experience is greater. Meanwhile, the listed criteria can be applied to many cases without much uncertainty. To be sure, the cyst of modern *Gonyaulax polyedra* (Nordli, 1951) shows none of the features listed above (although its rupture has not been described). Therefore, it is reasonable to expect that some fossil dinoflagellate cysts will also remain "hidden" in one or another of the genera of undifferentiated hystrichospheres.

In answering the second question, a fossil that can be recognized as a dinoflagellate is a cyst rather than a motile stage if—

1) The structures pointing to dinoflagellate affinity (see item 3 above) are not typical of a motile stage. For example: (a) If a girdle that could have received a transverse flagellum is not present, although a girdle may be reflected by the distribution of ornament or by special processes; (b) If the tabulation is indicated by the rupture line only or by ornamental structures, rather than by true sutures.

2) Structures are present that indicate the fossil was formed inside an enclosing cell wall.

These criteria, too, can be applied in many cases without much uncertainty. However, in other cases the question cannot be decided until the critical morphological features become better known. Some of the uncertain cases, such as *Odontochitina,* are discussed in the following section on selected taxa. Another uncertain case is *Gonyaulax.* In many species of this latter genus the plate boundaries, including those that cross the girdle, are provided with membranes that rise perpendicularly from the theca. How high must these be before they imply that the girdle was not functional? Do forms, with high membranes really intergrade with others as they seem to? If so, what does this mean? These questions must await more evidence.

In the list that appears on page 401 of this paper, these two sets of criteria have been applied to most of the described genera of fossil dinoflagellates and hystrichospheres. The following is a summary of the data in that list.

One hundred twelve genera of fossils are considered in detail. These were originally described as dinoflagellates, as hystrichospheres, or as incertae sedis. On the basis of the criteria applied here: thirty-nine genera, originally described as dinoflagellates, are considered motile stages; forty-three are considered dinoflagellate cysts, fourteen of which were originally described as dinoflagellates, seventeen as hystrichospheres, and twelve as incertae sedis; and thirty remain in an undifferentiated category. The genera of the latter group do not show dinoflagellate-like features. They include all the Paleozoic hystrichospheres and all those that range from the Paleozoic into younger strata, as well as twelve known only from the post-Paleozoic. In addition to these 112 genera, the names of twenty-one more are given. They, too, have been listed in the literature as dinoflagellates, hystrichospheres, or possibly related forms of uncertain position. They are not considered further here for one of two reasons: (1) Either the morphology of the fossils is too poorly understood to permit useful analysis without careful re-examination of type material, or (2) the skeletons are entirely calcareous or siliceous. Some of the same morphological features are known in these genera as in those that are treated in detail, and all of the genera with inorganic skeletons are definitely dinoflagellates. However, they are known from very few occurrences and are not normally recovered along with the fossils of organic composition.

DISCUSSION OF SELECTED TAXA

The characteristics of several selected fossil dinoflagellates and hystrichospheres have just been discussed in developing the new concepts presented in this paper.

Now, other selected taxa will be discussed (1) to show how these concepts apply on a broad scale, and (2) to point out some of the principal questions and problems that await further study. Of special note in the second regard are: the problem of homeomorphy in the formation of an enclosing network (see *Cannosphaeropsis*), the problem of a cyst within a cyst (see *Odontochitina*, etc.), and the question of primary versus secondary symmetry (see *Areoligera*).

Triblastula O. Wetzel, 1933
Plate 6, figures 6–8; plate 7, figures 4–6

Triblastula is a strange genus whose morphology is particularly significant in the present discussion. Unfortunately, it has never been thoroughly described and illustrated. The essential features are shown in the illustrations, which portray a species very similar to the type. *Triblastula* is, in effect, half hystrichosphere and half dinoflagellate in appearance. The central structure is hystrichosphere-like. A precingular archeopyle adjoins a girdle-like structure defined by rows of processes. On the side opposite the archeopyle a group of small processes suggests the ventral area. Toward the poles the tips of processes like those nearer the girdle support two outer surfaces (pl. 7, fig. 5). These polar structures are like the extremities of many motile dinoflagellates: the apical one tapers into a long horn with a terminal pore; the antapical one has a short closed point. Abbreviated versions of these terminal projections are visible on the cyst as small protrusions, one at each pole.

I interpret this to be an encysted dinoflagellate in which at least the polar portions of the fossil preserve the original outer wall of the motile stage. The central, spherical portion is the cyst proper. It is interesting to compare this structure with that described by Nordli (1951) for *Gonyaulax polyedra*, a modern species. In *Triblastula*, however, the polar structures on the outer wall are consistently fused with the tips of the spines on the cyst. In *G. polyedra* the adherence of the epitheca to the cyst seems to have been accidental.

Palmnickia Eisenack, 1954
Plate 6, figures 10–13; plate 7, figure 3

Palmnickia lobifera Eisenack appears to be a cyst somewhat like *Forma F*. The cyst wall, with large precingular archeopyle, was supported against the outer original wall by a system of lamellae and filamentous projections whose outer limits now record the dinoflagellate-like shape of that wall.

I have also studied the specimens referred to by Eisenack (1954) as "*Palmnickia* sp. indet." in the text (1954, p. 70) and as "*Palmnickia* sp., ex aff. *P. lobifera*" in the plate explanation (his pl. 12, fig. 20). The latter form has an apical archeopyle and its basic morphology suggests *Areoligera*. It is not, in my opinion, closely related to *Palmnickia* and is therefore discussed separately below.

Chlamydophorella Deflandre and Cookson, 1955

Scriniodinium trabeculosum Gocht, 1959
Plate 7, figure 9

These forms appear to consist of subspherical cysts supported within a thin-walled motile stage. Their morphology, therefore, suggests that of *Hystrichosphaeridium* and *Hystrichosphaera*. In *Chlamydophorella* and *Scriniodinium trabeculosum*, however, the outer wall is still present and the processes are more numerous, shorter, and more slender. Since I have not seen an actual specimen of *Chlamydophorella*, my interpretation is based on the illustrations and descriptions given by Deflandre and Cookson (1955, pp. 56–57, pl. 11, figs. 1–3). I have examined *Scriniodinium trabeculosum*, however. Gocht's illustrations (1959, pl. 4, fig. 5; pl. 8, fig. 2) show the two walls connected by tiny processes. He notes (p. 63) that these tend to be aligned along plate boundaries. An archeopyle has not been observed in *Scriniodinium trabeculosum*, nor in the type species of *Chlamydophorella*. Cookson and Eisenack (1960) report an "uneven break at one end" in a second species of *Chlamydophorella*, *C. urna*.

Hystrichosphaeridium Deflandre, 1937, emended, Eisenack, 1958
Plate 3, figures 15–19; plate 4, figures 1–6, 9–10; plate 5, figures 8–12

Many morphological variations occur in this large genus. Some of these have already been discussed. The following is a summary of pertinent observations:

1) In some species the girdle is reflected by a row of processes like the rest. This is illustrated by the "tubiferum group" as represented here by *H. recurvatum* (White) (pl. 4, figs. 1–3; pl. 5, fig. 8). In other species, the girdle is marked by a barren zone without any processes. Examples of this type are the forms illustrated here (pl. 4, figs. 6, 9–10) and others, such as: *H. complex* (White) as figured by Gocht (1959, pl. 3, fig. 2), *H. anthophorum* Cookson and Eisenack (1958, pl. 11, fig. 12, holotype), and *H. dictyophorum* Cookson and Eisenack (1958, pl. 11, fig. 14, holotype). In still other species, the girdle is reflected by processes that are structurally distinct from the rest, commonly more slender, and with less complex tips. An excellent example of this type is a species identified by Eisenack (1958, pl. 26, figs. 1–2) as *H. anthophorum*. However, Eisenack's specimens differ from the type of *H. anthophorum* in possessing a distinct row of girdle processes, as shown especially well by another specimen from his material (pl. 4, fig. 5). The character of the girdle processes, or their absence, is a taxonomic criterion that should be useful in reconsidering the generic assignment of forms now placed in *Hystrichosphaeridium*.

2) Details of the morphology, the quality of preservation, and the stage of development in the cyst itself all affect the ease with which the morphology can be interpreted. For example: (a) If the cyst is not ruptured,

which is often the case, the apical archeopyle cannot be identified. However, although the apical region is still present, a distinctively shaped crack can often be seen around part of its circumference. (b) Crumpling or tearing may obscure the archeopyle. In such cases polygonal boundaries to parts of the wall may provide clues to its existence and position. (c) Long, numerous, and irregularly compressed processes may make it difficult to recognize a girdle zone devoid of processes.

3) The evolutionary development of the processes in *Hystrichosphaeridium* will probably become clear as their structure is studied further. Two alternatives appear likely: (a) that the tubular processes of species like *H. tubiferum* resulted from the fusion of thin solid processes that migrated from the margins toward the center of the plate areas, or (b) that the central tubular processes were primitive, later subdividing into thin solid processes whose points of attachment to the wall migrated toward the margins of the plate areas. I suspect the former is the correct explanation, but more observations are needed. Dr. Charles Downie (1959, personal communication) independently arrived at similar thoughts regarding evolution of the processes.

4) Whatever the origin of the processes, it is clear that in *Hystrichosphaeridium* and its allies the processes are typically "plate-centered," in contrast to *Hystrichosphaera* and its allies, in which the processes rise from the plate boundaries, usually at their intersections. The vastly greater number of processes in typical *Hystrichosphaera* than in *Hystrichosphaeridium* is related to this feature. Some *Hystrichosphaeridium*, however, also have many more processes than they would have if each process corresponded to one plate. The explanation of these supernumerary processes in some species of *Hystrichosphaeridium* requires further study.

5) Extensions from the tips of processes commonly occur. In the "tubiferum group," the digitate margins of the processes may taper out into short thin strands. In *H. anthophorum* the funnel-like tips may be large and perforated by holes of varying size. In other types (e.g., pl. 4, figs. 9–10) the perforations occupy most of the area and the funnel wall is reduced to several rodlike elements joined at their tips. In some instances the margins of the funnel become ill-defined, and short strands extend out from it. I believe these strands formed, like the tips of the processes themselves, against the inner surface of the original outer wall of the cell. If the strands from one process are long and fused with those of its neighbors, the resulting morphology is one that has usually been considered diagnostic of the next genus, *Cannosphaeropsis*.

Cannosphaeropsis O. Wetzel, 1933
Plate 4, figures 11–13, 17

In a number of hystrichospheres of widely different geologic age, the main body is enclosed in a more or less concentric network of fine strands that join the tips of the processes. In one type, this morphology seems to have originated by modification of the processes in *Hystrichosphaeridium*, as suggested in the preceding section. The well-known species, *C. aemula* (originally *Hystrichosphaeridium aemulum*), is virtually transitional between typical *Hystrichosphaeridium* and typical *Cannosphaeropsis*. The angular margin of the apical archeopyle can be recognized in many published illustrations of *Cannosphaeropsis* species which have been reported from the Jurassic to the Eocene. In *C. utinensis*, the type species, and a closely similar form (pl. 4, fig. 17), the processes are greatly reduced in number and massiveness, and the enclosing network is highly developed. In these species the apical archeopyle is usually difficult to see because many specimens are either unruptured or intensely crumpled.

Some forms that are otherwise like *Hystrichosphaera* (i.e., with a precingular archeopyle, girdle, reflected plates, branched processes, etc.) resemble *Cannosphaeropsis* in possessing an enclosing network. A Miocene species of this sort is the type of the genus *Nematosphaeropsis* Deflandre and Cookson (1955), but a similar morphology also occurs in the Cretaceous and Eocene.

Plate 4, figs. 12–13, show a Jurassic species in which intricate trabeculae rise from the margins of platelike areas on the central body and support a network which, in some specimens, also reveals a pattern of plates and girdle. Although many specimens at first glance suggest *Cannosphaeropsis*, the archeopyle is precingular rather than apical.

Finally, pl. 4, fig. 11, illustrates a Middle Silurian hystrichosphere with a basic morphology strikingly suggestive of *Cannosphaeropsis*: central body with long processes supporting a network of fine strands connecting their tips. However, in this case there is no trace of other features that might suggest affinity with the three preceding forms.

All these examples indicate that the inner body was formed within an outer wall and was supported against it by processes connected at their tips by a network of strands. The morphology of the inner body (the cyst proper) in the first three suggests they are dinoflagellate cysts. The last example reflects parallel development of the enclosing network in an organism at most very distantly related to the others and perhaps coming from an entirely different group of organisms.

In summary, it appears that a number of distinctive morphological types occur among the dinoflagellate cysts that are now referable to *Cannosphaeropsis* because they bear connected processes *per se*. A useful taxonomic subdivision of this assemblage into separate genera should consider: (1) the type of archeopyle, (2) the structure of the processes, and (3) the nature of the interconnections between processes — i.e., whether between members of a group of processes that reflect a single plate (e.g., pl. 4, fig. 9), between processes that reflect different plates (e.g., *Cannosphaeropsis aemula* of Cookson and Eisenack, 1958, pl. 7, fig. 5), between processes aligned along plate boundaries (e.g., pl. 4, figs. 12–13), etc.

Odontochitina Deflandre, 1937

Wetzeliella Eisenack, 1938

Deflandrea Eisenack, 1938

Plate 1, figures 1–4; plate 2, figures 1–4; plate 6, figures 14–16; plate 8, figures 3–7

Although *Odontochitina* was originally described as incertae sedis, Deflandre noted that its striking outline gave it the aspect of a dinoflagellate. However, other dinoflagellate-like features were not apparent: no tabulation was recognized and no girdle was visible. By application of the principles discussed in this report, I believe *Odontochitina* (pl. 6, figs. 14–16) may be logically interpreted as a dinoflagellate cyst. The external structure is basically similar to *Forma B*, but it has one long apical and two antapical horns in the locations typical for many dinoflagellates. The margin of the rupture that divides the body into unequal parts is in the normal position for an apical archeopyle, but only occasionally shows a zigzag course or clefts suggesting plate areas. The smooth wall, without trace of a girdle or tabulation (aside from the rupture line), suggests that this is a cyst, rather than the theca of a motile stage. However, if this is so, it is not just a simple cyst. An inner wall (especially distinct at the horn bases) forms a second cystlike body within the outer one, implying that the whole is a cyst within a cyst.

The possibility of such a phenomenon (known to occur in some modern dinoflagellates) is suggested by other fossils. *Wetzeliella* (with an intercalary archeopyle) is one of these. It is difficult to conceive of *Wetzeliella* (pl. 8, figs. 3–7) as a swimming dinoflagellate, although it has conspicuous dinoflagellate-like features. The girdle (when it is indicated) runs around the extreme lateral projections of the elaborate outline. To follow this course the transverse flagellum would have had a most inefficient, if not wholly nonfunctional, orientation. Furthermore, a number of species, including *W. articulata* and *W. clathrata*, have surface projections that suggest contact with an enclosing membrane (possibly present in fragmentary form in some specimens, like pl. 8, fig. 7). In *W. articulata* the spines have T-shaped tips and are graded in length in a manner that would adjust them to contact with a surrounding wall that "rounds off" some of the angular outlines of the body. In *W. clathrata* many processes are joined in fencelike rows by a list or bar along their tips. I believe these features are fundamentally analagous, respectively, to the isolated processes in *Hystrichosphaeridium* and the interconnected ones in *Cannosphaeropsis*. If this interpretation is accurate (and it is made with some hesitance because of the problem that it raises), then the outer wall of what we know as *Wetzeliella* was a cyst, and the inner structure that is usually developed was a cyst within this cyst. The inner cyst appears to have developed by the same sort of contraction as in *Deflandrea*. This is shown by the correlation between the thickness of the wall of the inner cyst and the size of the inner cyst relative to its enclosing structure: the smaller the inner cyst, the thicker its wall, as shown by the sequence of figs. 5, 3, and 7, on pl. 8.

The problem raised by interpreting *Wetzeliella* as a cyst within a cyst is that other features of the morphology of *Wetzeliella* ally it closely with *Deflandrea*, and there is little about the morphology of *Deflandrea* to suggest that the outer wall is not the original exterior. Seemingly transitional forms exist between the two genera, and the two have been placed in the same family (Eisenack, 1954). Nevertheless, the possibility of the cyst-within-a-cyst condition merits careful study. Dr. Gerhard Alberti (1959, personal communication) informs me that he has one well-preserved specimen of *Deflandrea* in which the exterior is covered by a very thin and delicate, often closely adherent membrane. This could conceivably represent an original outer wall with the first cyst (i.e., the exterior of the fossil we usually see) formed close within it. Support for the same interpretation may come from *Xenikoon* Cookson and Eisenack, a genus resembling *Deflandrea* in several conspicuous features. Cookson and Eisenack (1960, p. 16) report and illustrate a specimen similar to Alberti's in that an outer, third membrane encloses the two that are usually found.

Other cysts within cysts are probably represented by *Dracodinium* Gocht, *Rhombodinium* Gocht, *Wetzeliella? neocomica* Gocht, *Muderongia* Cookson and Eisenack, and *Forma G*.

Wetzeliella? neocomica Gocht, 1957

Forma G

Muderongia Cookson and Eisenack, 1958

Plate 7, figure 10; plate 8, figures 1–2

These forms have outlines strongly suggesting relation to the dinoflagellates. However, their shape and structure show even more clearly than *Wetzeliella articulata* and *W. clathrata* that they could hardly have had functional transverse flagella. They are more plausibly interpreted as cysts; but if they are, an inner cyst occurs within the outer one, as in *Wetzeliella* and *Odontochitina*.

Wetzeliella? neocomica has a spinose exterior and an internal cyst. *Forma G* (pl. 8, figs. 1–2) is externally very similar to Gocht's species but has not yet been seen to contain an inner cyst (reflecting a different stage of development at time of death?). Both possess an apical archeopyle in contrast to the intercalary one in *Wetzeliella*—one of several features responsible for Gocht's uncertainty about the generic assignment.

Muderongia (pl. 7, fig. 10) combines features of *Wetzeliella? neocomica* and *Odontochitina*. The general outline, with conspicuous lateral horns (but with one of two apical horns greatly reduced), resembles the former; the smooth exterior surface and the close contact of the inner cyst with the outer wall resemble

the latter. An apical archeopyle is clearly visible in the illustrations of Cookson and Eisenack (1958, pl. 6, figs. 1–4), and a girdle is distinct in some specimens.

Cyclonephelium Deflandre and Cookson, 1955
Tenua Eisenack, 1958

Plate 1, figure 22; plate 5, figures 1–2

Gocht (1959, pp. 77–78) points out and briefly discusses the similarities between these two genera. He also emphasizes the importance of noting and comparing the details of their rupture. He observes that in both genera rupture takes place along a preformed suture. In the illustrations given here, (and also in some of those presented by Deflandre and Cookson, 1955; Eisenack, 1958; and Gocht, 1959) the zigzag break, with short clefts at the re-entrant angles, is clearly visible. The basic morphology is the same as that of the cyst in *Forma C* and in the genus *Aptea* Eisenack. (See also the discussion of flattening and symmetry under *Areoligera*.)

Deflandre and Cookson originally described the central bare region in *Cyclonephelium compactum*, the type species, as "polar" and the marginal ornamented band as "equatorial". The revised interpretation of orientation presented by Cookson and Eisenack (1960) agrees with the clues to a standard dinoflagellate orientation; for example, the traces of the precingular plates along the rupture line and the reduced antapical horns.

Many fossils with variable and perhaps intergrading morphological details seem referable to these genera, which I interpret as dinoflagellate cysts. Both whole and ruptured specimens occur. The archeopyle is apical. Specimens tend to be dorsoventrally flattened and to have a spinose ornament. In some specimens, spines are short and pointed; in others they are T-shaped and suggest contact with an original outer wall; in still others they are complexly interconnected at their tips. The projections may be evenly distributed, may be aligned to suggest plate boundaries, or may be reduced in the central parts of dorsal and ventral surfaces. A local convexity or a short point may suggest an apical horn. The antapical outline frequently shows two convexities with a depression between, suggesting modified antapical horns. In some cases only one antapical convexity is present, and some have a virtually circular outline.

The apical archeopyle of *Cyclonephelium compactum* is clearly shown by the illustrations of Deflandre and Cookson (1955, pl. 12, figs. 7–8).

Among the original specimens of *Tenua hystrix* (type species of the genus) studied by Eisenack (1958, p. 410), the opening varies from oblique to perpendicular to the long axis of the oval test. I believe this variation results merely from irregular compression of the thin-walled specimens. I interpret the opening as an apical archeopyle. Its margin is consistently parallel (or nearly so) to a reflected girdle delineated by rows of small spines. This girdle is recognizable in many specimens (including the holotype, pl. 1, fig. 22), but only occasionally are the boundaries between major plates also distinctly marked by rows of spines. The subequal edges of precingular plates are indicated in many specimens by the angulations in the archeopyle margin.

Systematophora Klement, 1960

Plate 4, figures 7–8; plate 9, figures 1–2

Klement (1960), in describing an Upper Jurassic assemblage of dinoflagellates and hystrichospheres, has pointed out a number of dinoflagellate-like characters in genera that he believes do not have affinities with the dinoflagellates. An example is his new genus *Systematophora*. In this genus he notes the occurrence of polygonal "fields" whose arrangement suggests a tabulation reminiscent of dinoflagellates. The processes typical of the genus occur in constant association with the outlines of these fields. He distinguishes between "dorsal" and "ventral" on the basis of the size and shape of the fields. In addition he recognizes a "girdle region".

Klement's keen observations on the morphology of these Jurassic types are a major contribution to our knowledge of the structure of Mesozoic hystrichospheres. I concur with his analysis of the morphology of *Systematophora* (whose structures are in many respects comparable to those of *Areoligera*), but not with his opinion regarding affinities of such genera. I interpret *Systematophora* as a dinoflagellate cyst whose "fields" and "girdle region" reflect the tabulation of a true dinoflagellate in the same fashion as other examples that have been discussed in this report.

In the type species, *S. areolata*, the processes are not connected at their tips and the fields from whose margins they rise are of relatively large diameter. In a second species, *S. orbifera* Klement, the processes of each group stand very close together, rising from a field of restricted diameter, and are complexly interconnected at their tips. The morphology of *S. orbifera* is similar to that of the form identified by Eisenack (1958*a*) as *Hystrichosphaeridium anthophorum* (illustrated here by pl. 4, fig. 5). Another morphological variation (pl. 4, figs. 7–8) suggests some features of *Areoligera*. In this case the fields are not completely encircled by the ridges from which the processes rise, and adjacent processes are occasionally fused together for some distance from their bases. Although the type species of *Systematophora* is highly distinctive, refinement of the generic limits will be necessary to clarify the relationship of the genus to *Hystrichosphaeridium* on the one hand and to *Areoligera* on the other, as evidenced by forms like the two just cited.

Additional comments on *Systematophora* will be found under the next genus, *Areoligera*.

Areoligera Lejeune-Carpentier, 1939
Plate 8, figures 11–15; plate 9, figures 3–7

The form illustrated here is very similar to the type species, *A. senonensis*, described by Lejeune-Carpentier, who carefully analyzed the morphology. Although she did not recognize an opening in her specimens, it is clear from her detailed descriptions and excellent illustrations that she was dealing with ruptured specimens with an apical archeopyle. She interpreted one apical "plate-field" to be present, while specifying that this was not visible. However, separate archeopyle covers (pl. 8, figs. 14–15; pl. 9, fig. 5) associated with the other specimens illustrated here reflect four apical plates.

I interpret *Areoligera* as a dinoflagellate cyst in which low membranes, extended into long finger-like processes, outline fields that reflect plates. The tabulation is distinct only on the dorsal surface, where three precingular (Lejeune-Carpentier's series "C"), three postcingular (series "B") and, probably, a single antapical plate ("E") are indicated. The girdle is reflected by small processes (series "A") between the pre- and postcingular series (compare with *Hystrichokolpoma* below). The ventral surface shows no tabulation, except along the archeopyle margin, where a total of six major plates (dorsal and ventral) are indicated by the rupture line. The ventral surface is outlined by a large discontinuous frill-like structure, similar to but more strongly developed than the structures around the dorsal plate-fields. Its major lobes suggest two precingular, two postcingular, and two posterior intercalary prominences (discussed further below). In uncompressed specimens (Lejeune-Carpentier, 1939) the ventral surface is flat or depressed, in contrast to a nearly hemispherical dorsal surface.

Comparison of *Systematophora* (pl. 9, figs. 1–2) and *Areoligera* (pl. 9, figs. 4–7) reveals some interesting and useful symmetry relationships. Klement (1960) noted the similarity between these genera. The processes in the type species of both are of the same distinctive sort; they outline platelike areas and reflect a girdle. Both genera have an apical archeopyle with a conspicuous notch in line with the ventral area (not mentioned by Klement in *Systematophora*, but recognizable in his photomicrographs). However, there are also conspicuous differences that are summarized under several headings below:

Dorsal plate fields

Systematophora: four precingular, about equal in size; three postcingular, larger than precingular; fields surrounded by processes equally developed on all sides of each field.

Aeroligera: three precingular, middle one larger than other two; three postcingular about equal to precingular in size; fields incompletely surrounded, processes reduced on side toward and enlarged on side away from dorsal midpoint of equator.

Ventral plate fields

Systematophora: two precingular, two postcingular, two posterior intercalary; all smaller than dorsal ones but encircled by similar processes.

Areoligera: no fields defined. Two multilobate flanges, one right and one left, have main enlargements in position of pre- and postcingular plates. Two smaller but similar projections correspond to intercalary fields of *Systematophora*.

Girdle processes

Systematophora: six plate fields, about evenly spaced.

Areoligera: variable, two to four developed, all on dorsal surface.

Antapex

Systematophora: evenly rounded, bearing circular plate field whose processes are equally developed on all sides.

Aeroligera: bilobed outline, with bilobate plate field; row of processes surrounding field interrupted on ventral side.

Equatorial cross section

Systematophora: about circular.

Areoligera: dorsal outline semicircular, ventral outline flat.

Symmetry of prominent surface structures

Systematophora: bilateral with respect to a plane passing through ventral area, between posterior accessory fields, and between plate areas on dorsal surface.

Areoligera: less perfectly bilateral with respect to a plane passing through 6″ on the ventral surface, and 3″ and 3‴ (i.e., the two central plate fields) on the dorsal surface, and between the lobes of the antapical field. The two accessory processes on the ventral side are asymmetrically positioned, the right-hand one lying astride the plane.

In *Systematophora*, with a virtually circular equatorial cross section, the primary dinoflagellate symmetry (bilateral with respect to a plane passing through the ventral area and the apices) is also revealed by the major surface features, i.e., the plate fields. In *Areoligera*, on the other hand, a flat ventral surface has developed at an oblique angle to the primary symmetry plane. As a result, the primary symmetry has been distorted and the ventral area lies far to one side of the ventral surface. Nevertheless, as in *Systematophora*, the major surface features show a bilateral symmetry, but this is a secondary symmetry in *Areoligera*, its plane passing through quite different structures than in *Systematophora*.

The biological explanation and implications of these observations are conjectural at the present state of our

knowledge. However, from a purely morphological point of view, they suggest additional ways in which we can analyze and compare the structure of fossil specimens. For example, a distortion of primary symmetry and a tendency toward dorsoventral flattening (similar to *Areoligera*) is shown by *Forma C*, *Cyclonephelium*, *Tenua*, and the form described by Eisenack as *Palmnickia* sp. ex aff. *P. lobifera* (see below). *Cyclonephelium* and *Palmnickia* sp. ex aff. *P. lobifera* (which I consider generically distinct from *Palmnickia*, see later discussion) also show a tendency toward reduction of the projecting structures on the ventral surface, as in *Areoligera*. An understanding of the disposition and development of the distinctive processes and plate fields in *Areoligera* and *Systematophora* helps in interpreting more highly modified forms like *Cyclonephelium* and *Palmnickia* sp. ex aff. *P. lobifera*.

Palmnickia sp. ex aff. P. lobifera Eisenack, 1954
Plate 8, figures 16–17; plate 9, figures 8–10

I have studied the four original specimens of this form. The one which Eisenack illustrated (1954, pl. 12, fig. 20) is refigured here, along with drawings. The form, which I interpret as a dinoflagellate cyst, has an apical archeopyle and shows marked similarities in basic morphology to *Areoligera* (compare pl. 9, figs. 8–10 with figs. 3–4, 7), particularly in shape and in the symmetry relationships of the processes. However, the processes differ in detail, being entire in *P.* sp. ex aff. *P. lobifera* instead of intricately digitate as in *Areoligera*. Other species soon to be described by Mrs. Ellen Müller (in press) seem to be intermediate between this form and *Areoligera* or to express other "variations on the same theme". Evaluation of the generic affinities of these types must await further study.

Hystrichokolpoma Klumpp, 1953
Plate 7, figures 7–8; plate 8, figures 8–10

I interpret *Hystrichokolpoma* as the cyst of a dinoflagellate whose plates are reflected by slender paired processes along the equator and by larger, hollow conical processes in the epi- and hypothecal areas. There is an apical archeopyle, with a conspicuous notch in its margin, marking the position of the ventral furrow.

In *H. cinctum*, the type species illustrated here, a tabulation of ?′, 6″, 6g, 5‴, 1⁗ is indicated. Processes reflecting plates 5″ and 1‴ are smaller than the others in each series. The ventral area is reflected by a group of processes of unequal size and irregular distribution. The largest, (almost as large as process 5″) lies immediately adjacent to the notch in the archeopyle margin and reflects the anteriormost plate of the ventral area. The others are much smaller and more slender. The girdle, reflected by the paired equatorial processes, is distinctly spiral.

Forma H
Plate 6, figure 9

This bizarre species, which I interpret as a dinoflagellate cyst, in a sense combines the characteristics of *Odontochitina* and *Hystrichosphaeridium*. Large chimney-like structures form one apical and two antapical horns. Smaller processes reflect the main plates of the epitheca and hypotheca. The ends of the processes are flared, suggesting that they formed as supports against an external wall (now missing), as in *Hystrichosphaeridium*. The processes are adjusted in length, depending upon their position, in such a way that the outer wall would have had a reasonable shape for a motile dinoflagellate. As in *Odontochitina*, an inner capsule is present, making it reasonable to consider *Forma H* a cyst within a cyst. The form named *Hystrichosphaera ceratioides* by Deflandre (1937) has a more or less similar morphology.

Aptea Eisenack, 1958
Plate 8, figure 18; plate 9, figures 11–12

After studying the original material of the type and other species, I interpret this as a dinoflagellate cyst with an apical archeopyle. The genus combines some of the salient morphological features of *Cyclonephelium* and *Forma D*. The exterior outline, as well as the shape and spacing of the main body within this outline, resemble *Forma D*. The numerous short and irregular processes, best developed in the peripheral areas of the dorsoventrally flattened specimens, recall *Cyclonephelium*. These processes probably contacted the outer wall of the motile stage. Fragments of this outer wall are, perhaps, represented by a tattered, membranous structure that, here and there, extends over the tips of the processes in some specimens. The outer wall is never as distinct and continuous as in *Forma D*. No true girdle is present, although its position is suggested in some specimens by the spacing and arrangement of processes. The basic morphology of the cyst proper (i.e., exclusive of the processes) is like *Forma C*; in other words, like *Cyclonephelium* or the cyst within *Forma D*.

Pareodinia Deflandre, 1947
Plate 8, figures 19–22; plate 9, figures 13–14

Originated for specimens similar to pl. 8, fig. 19, the generic concept could reasonably be extended to include the other forms illustrated here. A single apical horn is present. The antapex is rounded or provided with two short prominences. A girdle may be suggested by faint surface markings or by absence of projections. Commonly the rupture that forms the apical archeopyle is incomplete, so that the apical part of the test is still present. The archeopyle margin seldom shows clearly the angular boundaries of plates. The combination of morphological features suggests this is a dinoflagellate cyst.

Broomea Cookson and Eisenack, 1958
Plate 9, figure 15

This genus may at first recall *Pareodinia* or *Odontochitina*, but its distinctive features include (1) rupture by an intercalary archeopyle, (2) two solid antapical horns with fibrous structure, and (3) no inner cyst. Some specimens have a nearly smooth wall; others show distinct traces of a girdle, precingular, postcingular, and apical plates. The tabulation demonstrates clearly the intercalary position of the archeopyle.

I would exclude from the genus the new species, *B. micropoda*, which Eisenack and Cookson (1960) recently described. This form resembles the forms here considered *Pareodinia* (pl. 8, figs. 20–21; pl. 9, figs. 13–14) except in size.

LIST OF DESCRIBED GENERA

The following list includes 133 genera of dinoflagellates, hystrichospheres, and incertae sedia. For all but the twenty-one genera enumerated under the third subdivision, the generic name is followed in succession by the name of the author, date of first description, known geologic range of the genus, and (in parentheses) a letter or letters showing in what category ("d" for dinoflagellate, "h" for hystrichosphere, "is" for incertae sedis) the genus was originally placed or what category it has been generally considered to represent. For the last twenty-one, only the author and publication date are given. Figures in parentheses are number of genera.

DINOFLAGELLATES (82)

A) Without observed rupture (25)
- 1) Motile Stage (14)
  - *Certatocorys* Stein 1833, Cret.—Rec. (d)
  - *Cometodinium* Defl. & Courteville 1939, Cret. (d)
  - *Cryptarcheodinium* Defl. 1939, Jur. (d)
  - *Diconodinium* Eis. & Cook. 1960, Cret. (d)
  - *Eodinia* Eis. 1936, Jur. (d)
  - *Ginginodinium* Cook. & Eis. 1960, Cret. (d)
  - *Gymnodinium* Stein 1878, Jur.—Rec. (d)
  - *Hystrichodinium* Defl. 1935, Cret. (d)
  - *Palaeoperidinium* Defl. 1934, Jur.—Ter. (d)
  - *Peridinium* Ehrenberg 1840, Cret.—Rec. (d)
  - *Phanerodinium* Defl. 1937, Cret. (d)
  - *Raphidodinium* Defl. 1936, Cret. (d)
  - *Toolongia* Cook. & Eis. 1960, Cret. (is)
  - *Wetzelodinium* Defl. 1936, Cret. (d)
- 2) Motile stage with cyst inside (2)
  - *Dingodinium* Cook. & Eis. 1958, Jur. (d)
  - *Palaeohystrichophora* Defl. 1935, Cret.—Ter. (d)
- 3) Simple cyst (8)
  - *Aiora* Cook. & Eis. 1960, Cret. (h)
  - *Coronifera* Cook. & Eis. 1958, Cret. (h)
  - *Ctenidodinium* Defl. 1938, Jur. (d)
  - *Cyclodictyon* Cook. & Eis. 1958, Cret. (is)
  - *Dioxya* Cook. & Eis. 1958, Cret. (is)
  - *Hystrichokibotium* Klumpp 1953, Ter. (h)
  - *Nematosphaeropsis* Defl. & Cook. 1955, Ter. (h)
  - *Stephodinium* Defl. 1936, Cret. (d)
- 4) Compound cyst (i. e., cyst within a cyst) (1)
  - *Ceratocystidiopsis* Defl. 1937, Cret. (is)

B) Theca ruptured along girdle (4)
- 1) Motile stage (4)
  - *Dinopterygium* Defl. 1935, Cret. (d)
  - *Nannoceratopsis* Defl. 1938, Jur. (d)
  - *Oodnadatia* Eis. & Cook. 1960, Cret. (d)
  - *Wanaea* Cook. & Eis. 1958, Jur. (is)

C) With an apical archeopyle (30)
- 1) Motile Stage (3)
  - *Canningia* Cook. & Eis. 1960, Jur. (d)
  - *Lithodinia* Eis. 1935, Jur. (d)
  - *Microdinium* Cook. & Eis. 1960, Cret. (d)
- 2) Motile stage with cyst inside (5)
  - *Ascodinium* Cook. & Eis. 1960, Cret. (d)
  - *Belodinium* Cook. & Eis. 1960, Jur. (d)
  - *Chlamydophorella* Cook. & Eis. 1958, Jur.—Cret. (d)
  - *Pseudoceratium* Gocht 1957, Cret. (d)
  - *Pseudodeflandrea* Alberti 1959, Ter. (d)
- 3) Simple cyst (20)
  - *Actinotheca* Cook. & Eis. 1960, Cret. (is)
  - *Aptea* Eis. 1958, Cret. (d)
  - *Areoligera* Lejeune-Carpentier 1939, Jur.—Ter. (h)
  - *Cannosphaeropsis* O. Wetzel 1933, Jur.—Ter. (h)
  - *Cyclonephelium* Defl. & Cook. 1955, Cret. (h)
  - *Dictyopyxis* Cook. & Eis. 1960, Jur. (is)
  - *Eisenackia* Defl. & Cook. 1955, Cret.—Ter. (d)
  - *Ellipsoidictyum* Klement 1960, Jur. (h)
  - *Epiplosphaera* Klement 1960, Jur. (h)
  - *Fromea* Cook. & Eis. 1958, Cret. (is)
  - *Histiophora* Klement 1960, Jur. (d? is)
  - *Hystrichokolpoma* Klumpp 1953, Cret?—Ter. (h)
  - *Hystrichosphaeridium* Defl. 1937 emend. Eis. 1958, Jur.—Ter. (h)
  - *Kalyptea* Cook. & Eis. 1960, Jur. (is)
  - *Palaeostomocystis* Defl. 1935, Cret. (is)
  - *Pareodinia* Defl. 1947, Jur. (is)
  - *Schematophora* Defl. & Cook. 1955, Ter. (is)
  - *Systematophora* Klement 1960, Jur. (h)
  - *Taeniophora* Klement 1960, Jur. (h)
  - *Tenua* Eis. 1958, Jur.—Cret. (h)
- 4) Compound cyst (i. e., cyst within a cyst) (2)
  - *Muderongia* Cook. & Eis. 1958, Cret. (d)
  - *Odontochitina* Defl. 1935, Cret. (is)

D) With an intercalary archeopyle (9)
- 1) Motile Stage (0)
  - None
- 2) Motile stage with cyst inside (3)
  - *Deflandrea* Eis. 1938, Cret.—Ter. (d)
  - *Omatia* Cook. & Eis. 1958, Jur. (is)
  - *Xenikoon* Cook. & Eis. 1960, Cret. (is)
- 3) Simple cyst (3)
  - *Broomea* Cook. & Eis. 1958, Jur. (d)
  - *Komewuia* Cook. & Eis. 1960, Jur. (is)
  - *Pyxidiella* Cook. & Eis. 1958, Jur. (h)
- 4) Compound cyst (i. e., cyst within a cyst) (3)
  - *Dracodinium* Gocht 1955, Ter. (d)
  - *Rhombodinium* Gocht 1955, Ter. (d)
  - *Wetzeliella* Eis. 1938, Cret.—Ter. (d)

E) With a precingular archeopyle (14)
1) Motile stage (5)
Apteodinium Eis. 1958, Cret. (d)
Gonyaulax Diesing 1866, Jur.—Rec. (d)
Leptodinium Klement 1960, Jur. (d)
Rhynchodiniopsis Defl. 1935, Cret. (d)
Palaeoglenodinium Defl. 1935, Cret. (d)

2) Motile stage with cyst inside (3)
Nelsoniella Cook. & Eis. 1960, Cret. (d)
Scriniodinium Klement 1957, Jur.—Cret. (d)
Triblastula O. Wetzel 1933, Cret. (h)

3) Simple cyst (6)
Hystrichosphaera O. Wetzel 1933 emend. Defl. 1937, Jur.—Rec. (h)
Palmnickia Eis. 1954, Ter. (h)
Pterodinium Eis. 1958, Cret. (d)
Spongodinium Defl. 1936, Cret. (d)
Trichodinium Eis. & Cook. 1960, Cret. (d)
Xenicodinium Klement 1960, Jur. (d? is)

4) Compound cyst (i. e., cyst within a cyst) (0)
None

NON-DINOFLAGELLATES (without observed opening or with a simple circular pylome) (30)

A) With an internal capsule (cyst?) (9)
1) Exclusively post-Paleozoic (9)
Cirrifera Cook. & Eis. 1960, Cret. (is)
Codonia Cook. & Eis. 1960, Cret. (is)
Diplofusa Cook. & Eis. 1960, Cret. (is)
Diplotesta Cook. & Eis. 1960, Cret. (is)
Disphaeria Cook. & Eis. 1960, Cret. (is)
Korojonia Cook. & Eis. 1958, Cret. (is)
Platycystidia Cook. & Eis. 1960, Cret. (is)
Pterocystidiopsis Defl. 1937, Cret.—Ter.? (is)
Trigonopyxis Cook. & Eis. 1960, Cret. (is)

2) Exclusively Paleozoic (0)
None

B) Without an internal capsule (cyst?) (21)
1) Exclusively post-Paleozoic (3)
Gillinia Cook. & Eis. 1960, Cret. (is)
Palaeotetradinium Defl. 1934, Cret. (d)
Pterospermopsis O. Wetzel 1952, Jur.—Ter. (h)

2) Paleozoic ranging into post-Paleozoic (7)
Baltisphaeridium Eis. 1958, Camb.—Ter. (h)
Cymatiosphaera O. Wetzel emend. Defl. 1953, Sil.—Ter. (h)
Leiosphaeridia Eis. 1958, Precamb.—Ter. (h)
Micrhystridium Defl. 1937, Camb.—Ter. (h)
Tasmanites Newton 1875, Ord.—Ter.? (is)
Tytthodiscus Norem 1955, Jur.—Ter. (is)
Veryhachium Deunff 1954, Ord.—Cret. (h)

3) Exclusively Paleozoic (11)
Anthatractus Deunff 1954, Dev. (h)
Aremoricanium Deunff 1955, Ord. (h)
Deunffia Downie 1960, Sil. (h)
Dictyotidium Eis. 1955, Ord.—Sil. (h)
Diornatosphaera Downie 1958, Camb. (h?)
Domasia Downie 1960, Sil. (h)
Estiastra Eis. 1959, Sil. (h)
Leiofusa Eis. 1938, Camb.—Dev. (h)
Lunulida Eis. 1958, Sil. (h)
Polyedryxium Deunff 1954, Dev. (h)
Pulvinosphaeridium Eis. 1954, Sil. (h)

The score of genera proposed by Timofeev (mostly in 1959) for Cambrian and Ordovician fossils would all fall into category B, 3 above.

GENERA NOT CONSIDERED (21)

A) Dinoflagellates, probably all motile stages (14)
1) With fully calcareous theca (8)
Bicarinellum Defl. 1948
Biechelerella Defl. 1948
Calcicarpinum Defl. 1948
Calcigonellum Defl. 1948
Calciodinellum Defl. 1947
Calciogranellum Defl. 1948
Calcipterellum Defl. 1948
Calcisphaerellum Defl. 1948

2) With fully siliceous theca (1)
Peridinites Lefevre 1933

3) Excluded for reasons stated (5)
Actiniscus Ehrenberg 1840. Represented by internal skeletal elements only; no indication of external form.
Blepharocysta Ehrenberg 1873. Only one indeterminate fossil species has been referred to this genus.
Ceratium Schrank 1793. The generic identity of the few fossil forms referred here is doubtful. No fossil with diagnostic features of *Ceratium* has been reported.
Podolampas Stein 1883. Only one indeterminate fossil species has been referred to this genus.
Palhistiodinia Defl. 1938. Only one specimen of imperfectly understood morphology is known; possibly the result of injury or malformation.

B) Hystrichospheroid cyst (1)
1) Excluded for reasons stated (1)
Galea Maier 1960. Distinctions from similar genera uncertain.

C) Not definitely dinoflagellates (6)
1) Excluded for reasons stated (6)
Dictyosphaeridium W. Wetzel 1952. Critical criteria not determinable from published descriptions ot illustrations.
Disphaerogena O. Wetzel 1933. Original definition and illustration not adequate to permit recognition.
Membranilarnax O. Wetzel 1933. Generic characters not clear (see Eisenack, 1959).
Palaeocryptidium Defl. 1955. Small spherical or ellipticalbodies reported only from the Precambrian of France.
Pleurozonaria O. Wetzel 1933. Exact morphology uncertain.
Samlandia Eis. 1954. Morphology not sufficiently distinct to determine critical features. Has an apical opening and may possibly be a dinoflagellate cyst with traces of the wall of the motile stage.

The distribution of genera into these categories follows the criteria set forth earlier in this paper. However, it must be emphasized that the interpretations of morphology indicated by this list are tentative. Many are based solely on published descriptions and illustrations, whereas actual specimens should be examined to ascertain critical morphological details. Nor is the list proposed as a classification, although the morphological features discussed here should eventually lead to a more satisfactory classification than any now available. The list is intended only as a convenient summary of the data given, organized to emphasize certain aspects of the morphology of these genera.

CONCLUSIONS AND RECOMMENDATIONS

I believe that the evidence presented here establishes that many hystrichospheres are dinoflagellate cysts. This idea is not new. Nordli (1951), Braarud (in Erdtman, 1954), and McKee et al. (1959), in studying samples from modern seas and Recent sediments, have identified as dinoflagellate cysts objects that are morphologically hystrichospheres. However, the idea has not been widely extended to fossils.

The concepts developed in this paper can be used to interpret a large number of fossil genera and species. Taken together these species and genera emphasize the widespread occurrence, the simplicity, and the uniformity of the basic morphologic features that are considered important in this discussion. They also suggest the great variety of modifications that occur, and point out a few of the chief uncertainties and questions that await further study.

The morphological features discussed in this paper (i.e., manner of rupture, indications of tabulation, and the structure and arrangement of the processes) should be carefully observed and recorded when fossil material is being studied. They provide additional bases for recognizing similarities and differences between genera and species, thus, becoming valuable in the day-to-day practical applications of paleontology. They also provide useful clues to the biologic affinities of these fossil organisms.

A thin-section study of the detailed structure of the hystrichosphere wall and, especially, of the processes should provide additional criteria of taxonomic value and also contribute to our understanding of affinities and ways of life. Such a study should be applied to free specimens of normal preservation (rather than to exceptional material like the Paleozoic specimens studied by Sannemann, 1955). The argument has been advanced (e.g., Klumpp, 1953) that hystrichospheres are not cysts on the grounds that the protoplasm within was in contact with the sea water without through the avenues of the processes. Clearly, processes of some hystrichospheres are hollow, but it is often impossible to be sure that the cavity of a process opens into the central sphere or to the exterior through the process tip. In some cases, it certainly does not (as Klumpp pointed out in discussing walls of two layers). However, such details should be clarified and documented through ultra-thin sections.

SOURCE AND DISPOSITION OF SPECIMENS

In accordance with my purpose of discussing the morphology of the fossils (rather than their taxonomy, nomenclature, and distribution) only limited data on age and locality of the illustrated specimens are given. Locality numbers listed in the plate explanations are explained below:

1) Maplewood shale, Middle Silurian, New York.
2) Middle Jurassic limestone pebble in glacial drift, East Prussia. See Eisenack, 1938.
3) Jurassic (probably Dogger), West Pakistan.
4) Curtis fm., Upper Jurassic (Oxfordian), Dinosaur National Monument, Utah.
5) Upper Jurassic (probably Oxfordian), Western Australia. See Cookson and Eisenack, 1958.
6) Upper Jurassic (Malm delta,) southwest Germany. See Klement, 1960.
7) Upper Jurassic, Denmark.
8) Dilkuna fm., Lower Cretaceous (Neocomian), West Pakistan.
9) Lower Cretaceous (Neocomian), northwest Germany. See Gocht, 1959.
10) Lower Cretaceous (Aptian), South Australia. See Cookson and Eisenack, 1958.
11) Lower Cretaceous (Aptian), northern Germany. See Eisenack, 1958a.
12) Lower Goru fm., Lower Cretaceous (Albian), West Pakistan.
13) Lower Cretaceous (Albian), Venezuela.
14) Lower Cretaceous, New South Wales, Australia. See Deflandre and Cookson, 1955.
15) Assise de Spiennes, Upper Cretaceous (Senonian), Belgium. See Lejeune-Carpentier, 1939.
16) Upper Goru fm., Upper Cretaceous (Senonian), West Pakistan.
17) Navesink fm., Upper Cretaceous (Maestrichtian), New Jersey.
18) Red Bank formation, Upper Cretaceous (Maestrichtian), New Jersey.
19) Vincentown fm., lower Eocene, New Jersey.
20) "Blaue Erde," lower Oligocene, East Prussia. See Eisenack, 1954.

The present location of the figured specimens is given in the following tabulation. "USNM" identifies slides deposited in the United States National Museum. The coordinates refer to the position of the specimen on these slides as measured in millimeters to the right (R) or left (L) and toward the top (+) or bottom (−) of the slide from an index circle engraved near the lower left corner of the cover glass at the center of an "×" in India ink. Specimens in other collections are identified by the name of the collection in the place of coordinates.

The USNM slides are strew mounts. The specimens are mounted on the under side of the cover glass with a water-soluble medium (polyvinyl alcohol or "CLEARCOL"). The cover glass is bound to the main slide with a xylene-soluble medium (Canada balsam or "PERMOUNT").

PLATE 1

FIGURE	SLIDE NO.	COORDINATES
1	USNM 139421	R6.4, +11.0
2	USNM 139421	R12.2, +9.7
3	USNM 139421	R5.2, +13.3
4	USNM 139421	R14.9, +11.1
5	USNM 139391	R20.9, +8.6
6	USNM 139395	R12.5, +7.7
7	USNM 139394	R21.3, +3.2
8	USNM 139404	R16.1, +10.4
9	USNM 139396	R20.3, +10.7
10–14	Dogger 16	Eisenack Coll.
15–16	USNM 139391	R12.3, +6.1
17	USNM 139389	R15.7, +10.5
18	USNM 139404	R14.0, +7.9
19	USNM 139404	R26.4, +10.3
20	USNM 139403	R13.6, +14.8
21	USNM 139405	R16.4, +12.6
22	Ob. Apt 4	Eisenack Coll.

PLATE 2

FIGURE	SLIDE NO.	COORDINATES
1	USNM 139421	R12.2, +9.7
2	USNM 139421	R5.2, +13.3
3	USNM 139421	R14.9, +11.1
4	USNM 139422	R15.3, +13.7
5	USNM 139389	R3.8, +7.0
6	Dogger 16	Eisenack Coll.
7	USNM 139411	R3.4, +6.2
8	USNM 139391	R12.3, +6.1
9	USNM 139404	R14.0, +7.9
10	USNM 139403	R14.4, +8.4
11	USNM 139404	R16.2, +6.5
12	USNM 139400	R4.5, +12.4

PLATE 3

FIGURE	SLIDE NO.	COORDINATES
1	USNM 139400	R22.7, +12.4
2	USNM 139402	R21.7, +10.2
3	USNM 139404	R16.2, +6.5
4	USNM 139399	R10.8, +13.1
5	USNM 139413	R15.2, +13.1
6–7	USNM 139415	R22.2, +14.6
8	USNM 139414	R0.7, +15.5
9	USNM 139402	R15.5, +8.8
10	USNM 139399	L6.0, +3.2
11	USNM 139403	R16.9, +12.1
12	USNM 139398	R20.2, +8.5
13–14	USNM 139403	R25.6, +11.7
15	USNM 139412	R15.0, +15.4
16	USNM 139411	R0.6, +5.5
17–18	USNM 139407	L3.7, +10.7
19	USNM 139408	R14.1, +2.1

PLATE 4

FIGURE	SLIDE NO.	COORDINATES
1	USNM 139416	R13.3, +5.4
2	USNM 139416	R1.0, +9.5
3	USNM 139416	R16.2, +12.1
4	Ob. Apt 21	Eisenack Coll.
5	Ob. Apt 23	Eisenack Coll.
6	USNM 139399	R14.2, +11.0
7	USNM 139401	R5.5, +8.9
8	USNM 139403	R2.2, +4.7
9	USNM 139406	R25.2, +15.2
10	USNM 139406	R24.2, +15.2
11	USNM 139392	R4.2, +5.4
12	USNM 139403	R10.6, +4.8
13	USNM 139403	R28.9, +10.7
14–16	USNM 139424	R4.1, +5.0
17	USNM 139417	R9.6, +5.9

PLATE 5

FIGURE	SLIDE NO.	COORDINATES
1	Ob. Apt 4	Eisenack Coll.
2	P16225	Nat. Mus. Victoria
3	USNM 139415	R22.2, +14.6
4	USNM 139413	R1.1, +2.9
5–6	USNM 139413	R15.2, +13.1
7	USNM 139398	R20.2, +8.5
8	USNM 139416	R16.2, +12.1
9–10	USNM 139407	L3.7, +10.7
11	USNM 139412	R15.0, +15.4
12	XVI–67	Lejeune-Carpentier Coll.
13–14	USNM 139424	R4.1, +5.0

PLATE 6

FIGURE	SLIDE NO.	COORDINATES
1	USNM 139425	R11.8, +10.9
2	USNM 139415	R14.0, +5.9
3	USNM 139424	R18.4, +6.6
4	USNM 139424	R4.0, −2.6
5	USNM 139424	R28.3, +12.5
6–7	USNM 139423	R5.9, +16.5
8	USNM 139422	R23.4, +16.0
9	USNM 139416	R11.7, +8.9
10–11	Ph. 16	Eisenack Coll.
12–13	Ph. 21	Eisenack Coll.
14	USNM 41480	R14.1, +6.4
15	USNM 139418	R26.3, +9.9
16	USNM 139418	R12.5, +2.3

PLATE 7

FIGURE	SLIDE NO.	COORDINATES
1	USNM 139424	R18.4, +6.6
2	USNM 139424	R4.0, +2.6
3	Ph. 16	Eisenack Coll.
4–6	USNM 139424	R5.9, +16.5
7–8	Ph. 30	Eisenack Coll.
9	124	Gocht Coll.
10	P17279	Nat. Mus. Victoria

PLATE 8

FIGURE	SLIDE NO.	COORDINATES
1	USNM 139409	R13.8, +14.6
2	USNM 139410	R19.2, +12.0
3	Ph. 21	Eisenack Coll.
4	Ph. 3	Eisenack Coll.
5	Ph. 16	Eisenack Coll.
6	Ph. 30	Eisenack Coll.
7	Ph. 21	Eisenack Coll.
8–10	Ph. 30	Eisenack Coll.
11–12	USNM 139419	R6.1, +11.3
13	USNM 139419	R10.5, +7.1
14–15	USNM 139420	R16.5, +7.4
16–17	Ph. 13	Eisenack Coll.
18	Ob. Apt 4	Eisenack Coll.
19	USNM 139393	R4.7, +12.1
20	USNM 139400	R17.1, +10.8
21	USNM 139426	R18.8, +12.4
22	USNM 139397	R10.2, +3.2

PLATE 9

FIGURE	SLIDE NO.	COORDINATES
1–2	PR1149–97	Univ. Tübingen
3–4	USNM 139419	R6.1, +11.3
5–7	USNM 139420	R9.5, +13.6
8–10	Ph. 13	Eisenack Coll.
11	Ob. Apt 4	Eisenack Coll.
12	Ob. Apt 29	Eisenack Coll.
13	USNM 139426	R18.8, +12.3
14	USNM 139400	R17.1, +10.8
15	P17284	Nat. Mus. Victoria

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EXPLANATION OF PLATES

PLATE 1

1–4 *Deflandrea* sp. Four specimens showing sequential development of cyst, beginning (fig. 1) before any trace of cyst is present; × 500. Compare pl. 2, figs. 1–4. Locality 18.

5 *Gonyaulax jurassica* Deflandre, showing precingular archeopyle, × 500. Locality 4.

6–7, 9 *Gonyaulax* sp. Three specimens ruptured along girdle. 6, Complete specimen in equatorial view, girdle continuous with hypotheca below rupture at right; 7, apical view of epitheca, without girdle; 9, equatorial view of hypotheca, with girdle; × 500. Locality 3.

8 *Gonyaulax* sp. Isolated cover of precingular archeopyle, × 500. Locality 7.

10–13 *Lithodinia jurassica* Eisenack. 10, Ventral view of entire specimen with archeopyle closed; 11–12, ventral views of specimen with open archeopyle, focused on ventral and dorsal surfaces; 13, ventral surface of another specimen, × 330; compare pl. 2, fig. 6. Locality 2.

14 *Forma A.* Ventral view of specimen with apical archeopyle, × 1250. Compare pl. 2, fig. 7. Locality 12.

15–17 *Forma B.* 15–16, Ventral and dorsal surfaces of specimen shown by pl. 2, fig. 8; 17, dorsal surface of another specimen; × 600. Locality 4.

18 *Forma C.* An entire specimen, × 550; compare pl. 2, fig. 9. Locality 7.

19–21 *Forma C.* Three specimens with open apical archeopyle, × 550. Note zigzag margin with notch (right of center) identifying position of ventral area. In figs. 20 and 21, faint parallel markings show reflected girdle, more distinct at different focus level that also reveals ventral area. Compare pl. 2, figs. 10–12. Locality 7.

22 *Tenua hystrix* Eisenack. Holotype (Eisenack 1958a, pl. 23, fig. 1), × 330. Note similarity to *Forma C;* compare pl. 5, fig. 1. Locality 11.

PLATE 2

1–4 *Deflandrea* sp. Four specimens showing sequential development of the cyst (stippled), × 750. The earliest stage, without any trace of the cyst, is not shown (see pl. 1, fig. 1). The cyst first appears (fig. 1, same specimen as pl. 1, fig. 2) as a thin-walled structure nearly filling the internal cavity. Other specimens (figs. 2–3, same specimens as pl. 1, figs. 3–4) show later, more contracted stages. As the cyst becomes more nearly spherical, the wall becomes thicker. The variant shown in figure 4 is atypical in clearly showing the position of the girdle. The precingular archeopyle is present and open in all specimens (including ones without a cyst). The cyst itself is not ruptured in any of the specimens illustrated. Locality 18.

5 *Gonyaulax jurassica* Deflandre, showing precingular archeopyle as typically developed in most fossil specimens of this genus by release of plate 3″, × 750. The narrow band surrounding the opening was originally part of plate 3′, showing that the line of rupture that formed the archeopyle is not exactly coincident with the sutural boundary of the original plate. Locality 4.

6–8 Apical archeopyle in three dinoflagellates with well-developed plates, girdle, and ventral area. Ventral views. 6, *Lithodinia jurassica* Eisenack (same specimen as pl. 1, fig. 13), × 500, locality 2; 7, *Forma A* (same specimen as pl. 1, fig. 14), × 1750, locality 12; 8, *Forma B* (same specimen as pl. 1, fig. 15, but image reversed), × 1000, locality 4.

9 *Forma C.* A nearly entire specimen (same as pl. 1, fig. 18), × 750. Crack outlines an apical archeopyle similar to that in *Lithodinia* and *Formae A* and *B.* However, plates are not clearly indicated, and girdle and ventral area are not recognizable. Locality 7.

10–12 *Forma C.* Three other examples with archeopyle open, × 750. Outline shape is variable (commonly with an antapical indentation and two adjacent asymmetrical bulges), but archeopyle is constant. 10, Surface originally smooth; 11, (same specimen as pl. 3, fig. 3), ornament of short spines omitted; 12, ornament of short spines omitted except for largest ones (shown by dots) which suggest outlines of girdle and ventral area. Locality 7.

PLATE 3

1–4 *Forma C.* Four distinct types; three specimens with archeopyle closed, one with it open; showing variations in outline shape and surface ornament, × 550. Locality 7.

5–8 *Forma D.* 5, Complete specimen, × 400; 6, apical portion only, showing zigzag rupture, × 400; 7, detail of same, showing support between cyst wall and theca, × 1000; 8, cyst alone, with only tattered remnants of adherent theca (note similarity to fig. 1), × 400. Compare pl. 5, figs. 3–6. Locality 12.

9–14 *Forma E.* 9–11, Three complete specimens with granulose cyst within thin theca, × 500; 12, specimen lacking apical portion of both cyst and theca and revealing zigzag archeopyle margin (compare pl. 5, fig. 7), × 500; 13–14, two focus levels of a fragment that shows correlation between sutures of thecal plates (marked by rows of minute processes) and the plate areas on the cyst as reflected by distribution of granules and angulations in the archeopyle margin, × 600. Reflected plate of cyst is smaller than corresponding plate of theca. Girdle, visible in fig. 14, is reflected by bare zone just above it on cyst; apical limit of precingular plate (digitate suture at top of fig. 13) is reflected by archeopyle margin of cyst. Locality 7.

15–19 *Hystrichosphaeridium* spp. 15, Cover of apical archeopyle; compare pl. 5, fig. 11. 16, Specimen with wall partly ruptured along archeopyle margin and between reflected precingular plates. A process rises from the center of each plate area defined by the rupture; equatorial zone is bare of processes. 17, 18, Two focus levels of a specimen showing similarity between polygonal tip of process (fig. 17, top center) and reflected precingular plate (fig. 18, same position); compare pl. 5, figs. 9, 10. 19, Another specimen with deep clefts extending from archeopyle margin between reflected precingular plates. All × 550. Figs. 15–16, locality 12; figs. 17–19, locality 8.

PLATE 4

1–3 *Hystrichosphaeridium recurvatum* (White). Three specimens showing development of apical archeopyle, × 550. 1, Apical region entire; 2, archeopyle partially open but cover, bearing four processes like the group at upper end of fig. 1, not displaced; 3, archeopyle open, revealing portions of polygonal outlines of reflected plates along its margin (compare pl. 5, fig. 8). Locality 16.

4–5 *Hystrichosphaeridium* sp. 4, Oblique view showing margin of apical archeopyle for comparison with fig. 3, × 235; 5, the large and complex precingular, postcingular, and antapical processes contrast with the equatorial row of slender processes having short bifurcate tips, × 330. Locality 11.

6 *Hystrichosphaeridium* sp. A complete specimen showing how processes may increase in complexity from apex to antapex, × 500. Four apical processes (on archeopyle cover) only slightly more complex than those of *H. recurvatum;* in contrast, those of hypotheca (girdle reflected by bare equatorial zone) rise from a basal ring and consist of numerous strands joined at their tips. Locality 7.

7–8 *Systematophora?* sp. A species with apical archeopyle (closed in fig. 7, open in fig. 8), simple processes along girdle and more complex processes elsewhere. Differs from typical *Systematophora* in that basal ridge from which each group of processes rises is not a complete ring. This feature and partial fusion of adjacent processes from a single plate area (fig. 7, upper right) suggest transition between *Systematophora* and *Areoligera.* Fig. 7, × 500; fig 8, × 400. Locality 7.

9–10 *Hystrichosphaeridium* sp. Apical views, focused on antapex and apex, × 400. 9, Small ringlike base of single complex antapical process is surrounded by four similarly complex processes of postcingular series and two simpler processes (on right) of ventral area. Girdle zone (out of focus) is bare. 10, Open apical archeopyle with one large precingular process (upper left) partly in focus rising from reflected precingular plate; a second precingular plate visible at left; two slender processes (only one in focus) mark ventral area (at right). Locality 7.

11–13 Homeomorphic development of *Cannosphaeropsis*-like structures, 11, A Silurian hystrichosphere, × 550, locality 1; 12–13, two extremes of a highly variable Jurassic species. A precingular archeopyle is well developed and, in simple variants (fig. 13), a girdle and tabulation are distinct, × 400. Locality 7.

14–16 *Hystrichosphaera* sp. Ventral views, focused on ventral surface, optical section, and dorsal surface; showing typical processes, reflected tabulation, and precingular archeopyle, × 600. Compare pl. 5, figs. 13, 14. Locality 19.

17 *Cannosphaeropsis* cf. *C. utinensis* O. Wetzel. Processes joined at their tips into an encircling network with distinctively forked short branches from its main lists, × 550. Locality 16.

PLATE 5

1 *Tenua hystrix* Eisenack. Outline drawings of the holotype (Eisenack, 1958a, pl. 23, fig. 1; this report, pl. 1, fig. 22) with surface ornament omitted, × 500. Locality 11.

2 *Cyclonephelium compactum* Deflandre and Cookson. Outline drawing of a paratype specimen (Deflandre and Cookson, 1955, pl. 2, fig. 13), with processes omitted, × 500. The same morphology is recognizable in the original illustration of the holotype. Locality 14.

3–6 *Forma D*, a dinoflagellate with a thin outer wall around an inner cyst (stippled), both structures ruptured to form an apical archeopyle (figs. 3, 5 are same specimens as pl. 3, figs. 5–6). 3, Isolated apical part; 4, isolated antapical part; 5, entire specimen, walls ruptured but not widely separated; 6, detail of connections between outer wall and inner cyst(in optical section) visible in fig. 3. Figs. 3–5, × 500; fig. 6, × 750. Locality 12.

7 *Forma E.* A specimen (same as pl. 3, fig. 12) in which both the inner cyst (stippled) and the wall of the motile stage are ruptured to form an apical archeopyle, × 1000. Granular ornament of cyst omitted except for coarse granules along archeopyle margin. In original specimen, rows of other coarse granules on cyst reflect the tabulation of motile stage shown by rows of hairlike processes. Locality 7.

8 *Hystrichosphaeridium recurvatum* (White). Drawing of the specimen shown in pl. 4, fig. 3, emphasizing distribution of processes by showing only basal portions of processes on one side and around open archeopyle, × 1000. Locality 16.

9–10 *Hystrichosphaeridium* sp. Two processes from a single specimen (shown by pl. 3, figs. 17, 18) showing structure of processes and their relations to cyst wall, × 2000. 9, A precingular process; outline of tip of process matches outline of polygonal area (stippled) of wall along archeopyle margin. 10, A postcingular process, also with polygonal tip; but reflected plate boundaries (suggested by dashed lines) are not visible on cyst wall. Locality 8.

11 *Hystrichosphaeridium* sp. Cover of apical archeopyle reflecting 4 plates, each with a central process (same specimen as pl. 3, fig. 15), × 750. Locality 12.

12 *Hystrichosphaeridium tubiferum* (Ehrenberg). A group of plates and processes illustrated by Lejeune-Carpentier (1939, text-fig. 4); probably an archeopyle cover reflecting a group of apical plates like those in fig. 11, × 1000. Smallest central process may reflect covering plate of apical pore. Locality 15.

13–14 *Hystrichosphaera* sp. A morphologically simple species with distinct tabulation, precingular archeopyle, and relatively few processes characteristically forked at the tips. Ventral views (same specimen as pl. 4, figs. 14–16); × 1000; 13, focused on ventral surface; 14, focused on dorsal surface. Locality 19.

PLATE 6

1–5 *Forma F.* Five different specimens, × 400; compare pl. 7, figs. 1, 2. 1, Dorsal surface with open precingular archeopyle; 2, optical section showing nature of large processes toward poles and spiral equatorial "shelf"; 3, ventral surface showing bases of small processes reflecting plates of ventral area between offset ends of reflected girdle; 4, lateral view of specimen with open archeopyle; 5, isolated archeopyle cover bearing two processes (only bases visible, lower one transversely elongate). Locality 19.

6–8 *Triblastula* cf. *T. utinensis* O. Wetzel. 6, Ventral surface showing reflected girdle and ventral area; 7, optical section of same specimen (innermost smoothly oval, light area is an artifact caused by optical discontinuity in mounting medium); 8, oblique view of dorsal surface of another specimen showing girdle and open precingular archeopyle; × 500. Compare pl. 7, figs 4–6. Locality 18.

9 *Forma H.* A typical specimen, showing characters suggestive of both *Hystrichosphaeridium* and *Odontochitina*, × 400. Apical archeopyle is cracked open but apex is not displaced. Locality 16.

10–13 *Palmnickia lobifera* Eisenack. 10–11, Views of paratype (Eisenack 1934, pl. 11, figs. 11–12) with closed precingular archeopyle. Compare pl. 7, fig. 3. 12–13, Similar views of holotype (Eisenack, 1934, pl. 11, fig. 10). All × 330. Locality 20.

14–16 *Odontochitina* spp. 14, Complete specimen with archeopyle ruptured but apex not displaced; 15–16, another species represented by isolated apical and antapical portions. All × 400. Fig. 14, locality 13; figs. 15–16, locality 16.

PLATE 7

1–2 *Forma F.* A dinoflagellate cyst with the girdle represented by a spiral shelflike projection, and large processes near the poles. Lengths of processes increase with distance from girdle. 1, Ventral view (same specimen as pl. 6, fig. 3); positions of archeopyle and girdle on dorsal surface are shown by dotted lines. 2, Lateral view (same specimen as pl. 6, fig. 4) in optical section; projected archeopyle margin and course of equatorial structure dotted; dashed lines joining tips of processes suggest position of original wall of motile stage. Note gradation in lengths of processes, especially the slender ones in the ventral area (right side of drawing). All × 500. Locality 19.

3 *Palmnickia lobifera* Eisenack. Drawing of paratype (Eisenack, 1954, pl. 11, fig. 11; this report, pl. 6, fig. 11) as seen in optical section, × 500; projected outline of precingular archeopyle shown by dotted line. Partially fused extremities of filamentous and membranous processes suggest outline shape of original cell; compare structure with that of *Forma F.* Locality 20.

4–6 *Triblastula* cf. *T. utinensis* O. Wetzel. Dinoflagellate-like apical and antapical horns are combined with a hystrichosphaeroid central structure; processes along girdle are bifurcate, elsewhere single. Ventral views (same specimen as pl. 6, figs. 6–7), × 750; 4, Focused on ventral surface, showing offset girdle and irregular processes reflecting ventral area; 5, optical section, showing two processes (one broken) beneath apical horn extending between inner cyst wall and thinner wall of apical horn; 6, focused on dorsal surface, showing girdle and precingular archeopyle (slightly distorted). Locality 18.

7–8 *Hystrichokolpoma cinctum* Klumpp. Drawings of hypotype (Eisenack, 1954, pl. 10, fig. 11; this report, pl. 8, figs. 8–10). The reflected tabulation is: ?′, 6″, 5‴, 1⁗. A notch in the margin of the open apical archeopyle indicates plate 1′ just above the large process that reflects the anteriormost plate of the ventral area. Ventral views, × 500; 7, focused on ventral surface; 8, focused on dorsal surface. Locality 20.

9 *Scriniodinium trabeculosum* Gocht. Based on pl. 8, fig. 2, of Gocht (1959), showing inner cyst (stippled) joined to the outer thin-walled theca by short delicate spinelike processes, × 600. Locality 9.

10 *Muderongia mcwhaei* Cookson and Eisenack. Holotype, based on pl. 6, fig. 2 of Cookson and Eisenack (1958), × 350. Course of girdle (dotted lines) derived from Cookson and Eisenack's pl. 6, fig. 4. h – reduced antapical horn. Locality 10.

PLATE 8

1–2 *Forma G.* Compare *Wetzeliella? neocomica* Gocht. 1, Specimen without apex, showing apical archeopyle; 2, complete specimen; × 400. Locality 8.

3, 5–6 *Wetzeliella articulata* Eisenack. 3, Holotype (Eisenack, 1938, text-fig. 4; 1954, pl. 7, fig. 1); 5, specimen with relatively large, thin-walled inner cyst; 6, specimen (Eisenack, 1954, pl. 8, fig. 15) with relatively small, thick-walled inner cyst; × 250. Note short spines with expanded T-shaped or Y-shaped tips. Locality 20.

4, 7 *Wetzeliella clathrata* Eisenack. 4, A typical specimen (Eisenack, 1954, pl. 7, fig. 13) showing short processes supporting narrow lists; 7, specimen whose processes seem to support a thin discontinuous membrane and are joined by solid lists only here and there, thus showing characters intermediate between typical *W. articulata* and typical *W. clathrata* and suggesting the presence of an original outer wall distal to the processes, × 250. Locality 20.

8–10 *Hystrichokolpoma cinctum* Klumpp. Ventral views of a typical specimen (Eisenack, 1954, pl. 10, fig. 11) focused at three levels: on ventral surface, optical section, and dorsal surface, × 330. Compare pl. 7, figs. 7–8. Locality 20.

11–15 *Areoligera* cf. *A. senonensis* Lejeune-Carpentier. 11–12, Ventral views of ventral and dorsal surface of one specimen with open apical archeopyle (compare pl. 9, figs. 3, 4); 13, dorsal surface of another specimen (archeopyle open) to show finger-like processes; 14–15, archeopyle cover at two focus levels to show processes and polygonal outline (compare pl. 9, fig. 5); × 400. Locality 18.

16–17 *Palmnickia* sp. ex. aff. *P. lobifera* Eisenack. Dorsal views of one specimen (Eisenack, 1954, pl. 12, fig. 20) focused on ventral and dorsal surfaces, × 330. Note similarity to *Areoligera* and compare pl. 9, figs. 8–9. Locality 20.

18 *Aptea polymorpha* Eisenack. Short irregular processes from inner wall (cyst) support thin and discontinuous outer membrane, × 330. Wall ruptured to form apical archeopyle, but apex not displaced. Compare pl. 9, figs. 11–12. Locality 11.

19–22 *Pareodinia* spp. Four complete specimens representing four distinct species. Rupture line of apical archeopyle visible in all but fig. 22. Figs. 19, 22, × 550; figs. 20–21, × 500. Fig. 19, locality 3; figs. 20–22, locality 7.

PLATE 9

1–2 *Systematophora areolata* Klement. Based on text-figs. 32 and 33 of Klement (1960). 1, Ventral surface; dotted line shows margin of apical archeopyle visible in Klement's pl. 9, fig. 2, but not shown by his drawings, in which the circular opening is suggested. 2, Dorsal surface. All × 650. Locality 6.

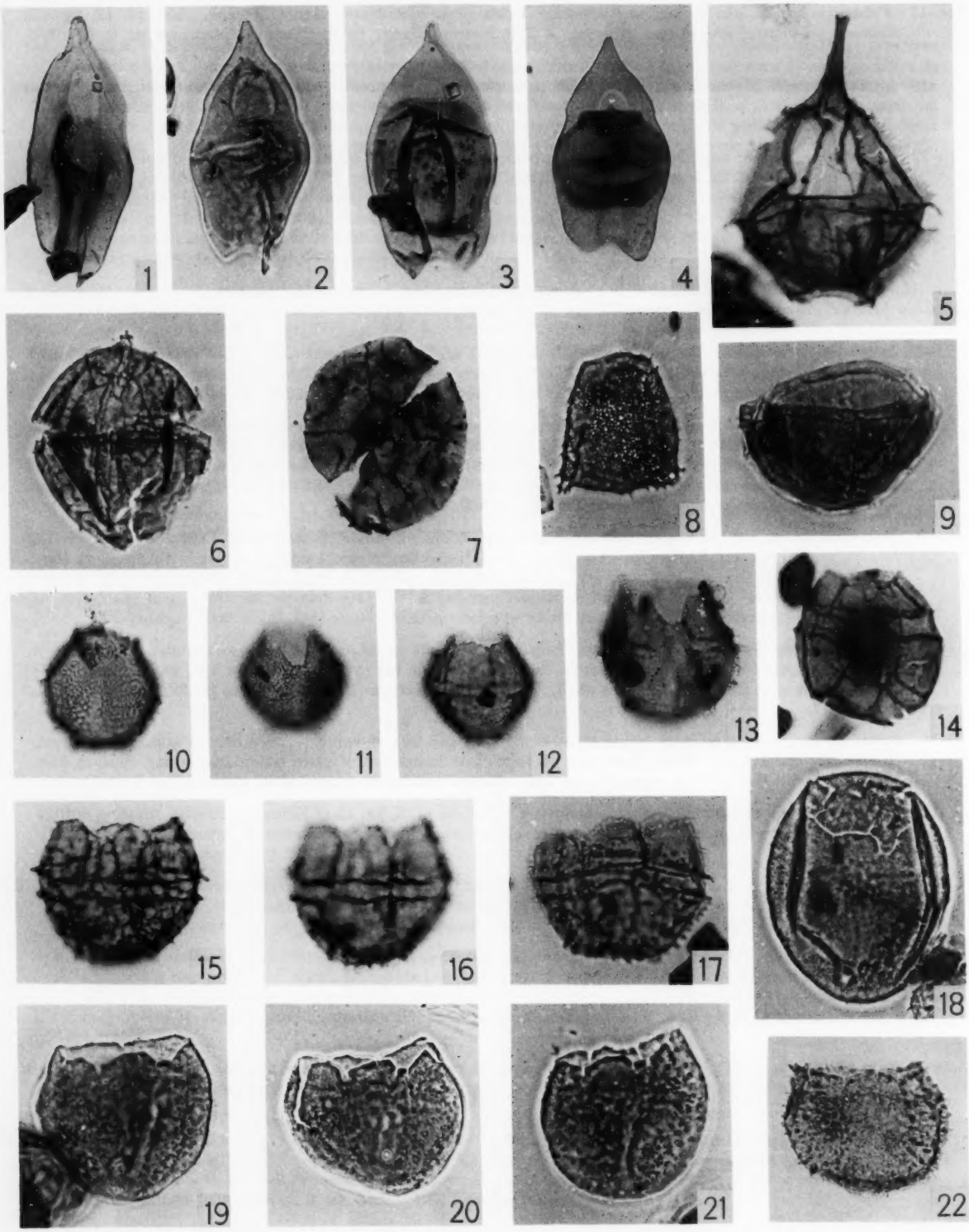
3–7 *Areoligera* cf. *A. senonensis* Lejeune-Carpentier. 3–4, Ventral views focused on ventral and dorsal surfaces (same specimen as pl. 8, figs. 11–12), × 650; 5, cover of apical archeopyle with reflections of four apical plates; only the bases from which the many finger-like processes arise are shown by hachures, × 500; 6–7, diagrams of ventral and dorsal surfaces showing bases of projections (hachures) and their correlation with tabulation indicated by margin of open apical archeopyle, × 500. Locality 17.

8–10 *Palmnickia* sp. ex. aff. *P. lobifera* Eisenack. Drawings of the specimen illustrated by Eisenack (1954, pl. 12, fig. 20) and by pl. 8, figs. 16–17 of this report. The chief morphological similarities are with *Areoligera* (figs. 3–7) and *Forma C* (e.g., pl. 2, figs. 11–12), rather than with *Palmnickia* (pl. 7, fig. 3). Dorsal views; 8, focused on ventral surface, × 500; 9, focused on dorsal surface, × 500; 10, diagram to show bases (hachures) of membranous processes on dorsal surface for comparison with *Areoligera* (fig. 7), × 400. Locality 20.

11–12 *Aptea polymorpha* Eisenack. The inner cyst (stippled), with an apical archeopyle, is surrounded by a complex of short processes (not shown here) that fill the space between the cyst and the outer line, which marks their tips. 11, Paratype (same specimen as pl. 8, fig. 18); 12, paratype (Eisenack, 1958a, pl. 22, fig. 6); × 400. Locality 11.

13–14 *Pareodinia* spp. Two specimens (same as pl. 8, figs. 21 and 20), showing rupture line of apical archeopyle, × 750. 13, Species with faint girdle but without clear indication of plate boundaries along rupture line. 14, Species with two short antapical horns and reflected tabulation suggested by rupture line. Locality 7.

15 *Broomea ramosa* Cookson and Eisenack. Holotype, based on pl. 3, fig. 15 of Eisenack (1958b), showing outline of precingular archeopyle (cover in place) and traces of girdle and other reflected tabulation, × 500. Locality 5.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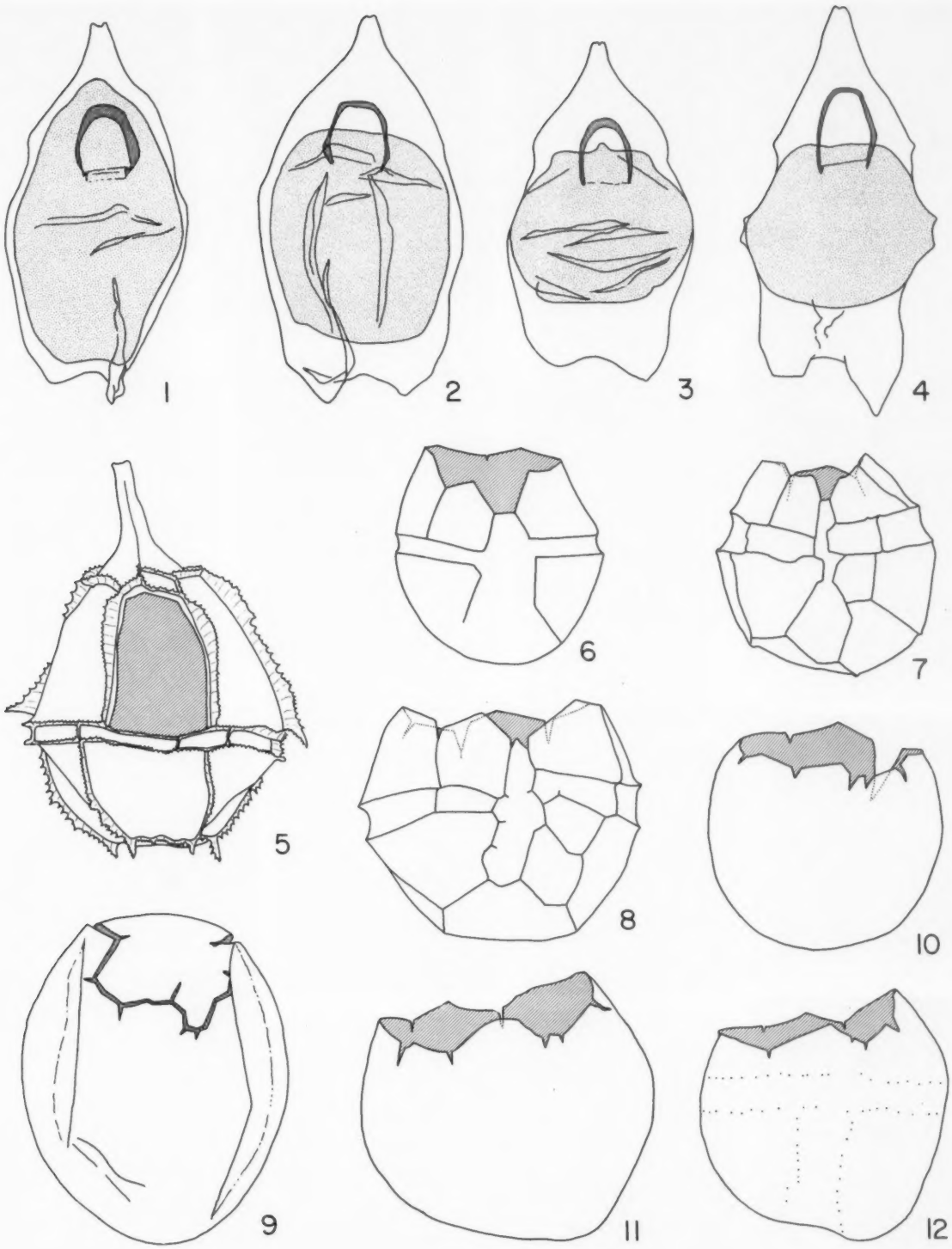
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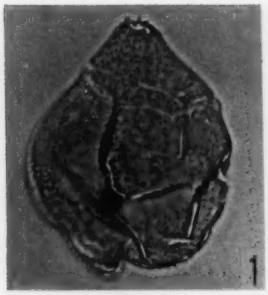
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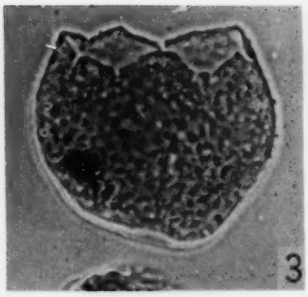
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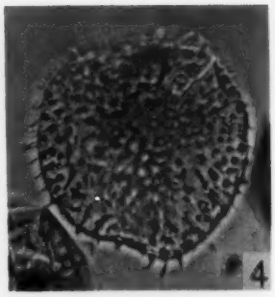
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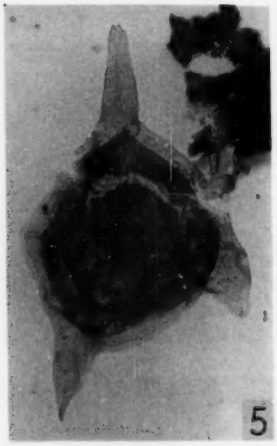
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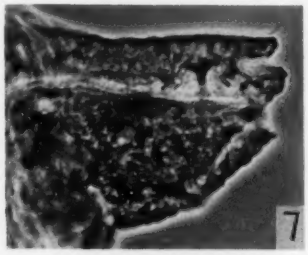
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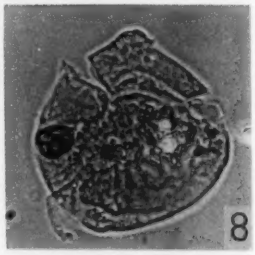
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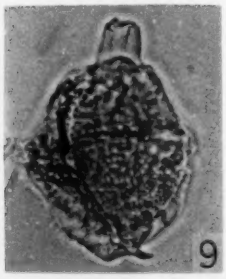
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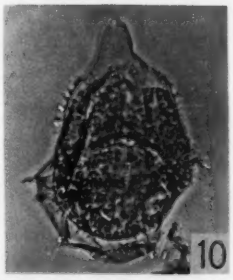
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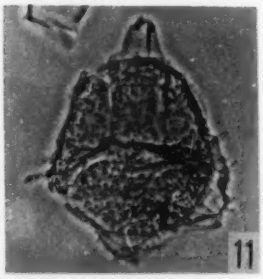
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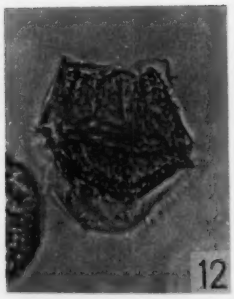
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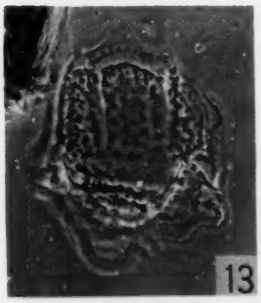
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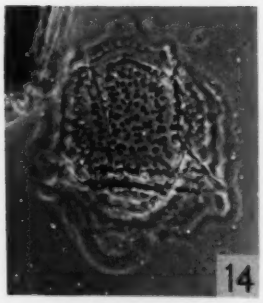
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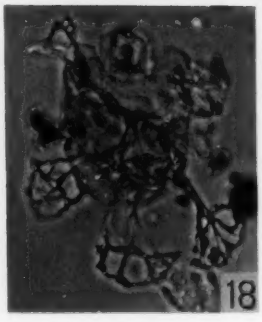
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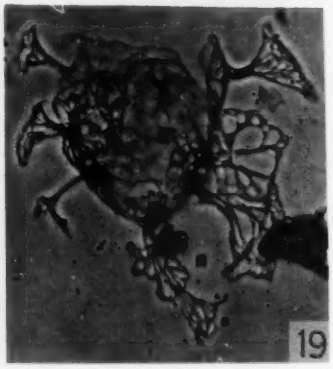
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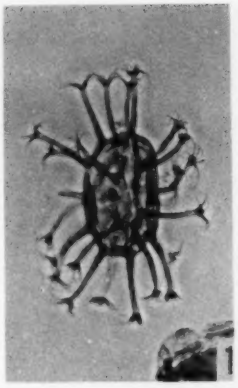
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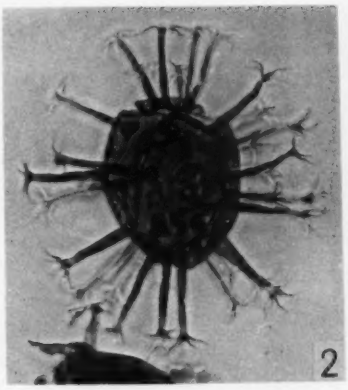
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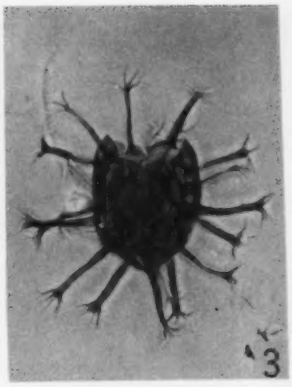
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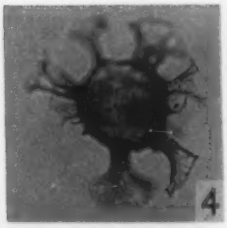
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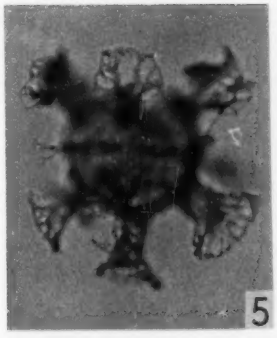
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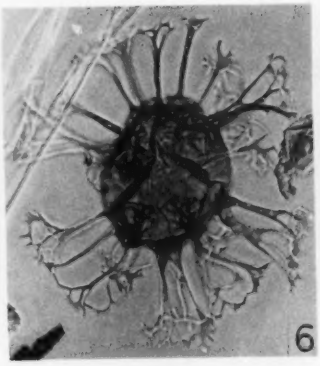
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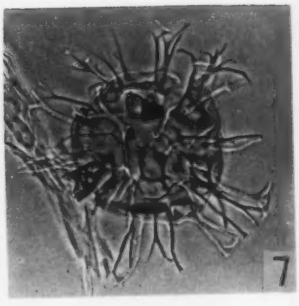
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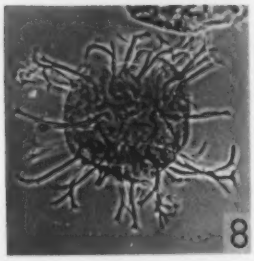
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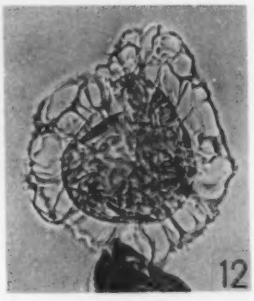
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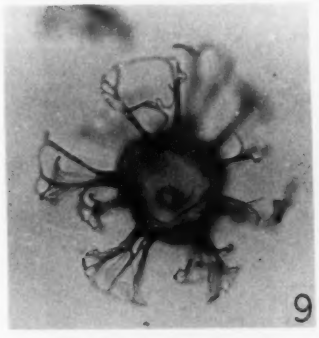
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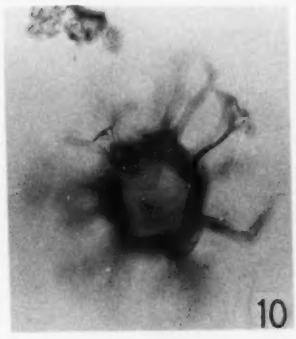
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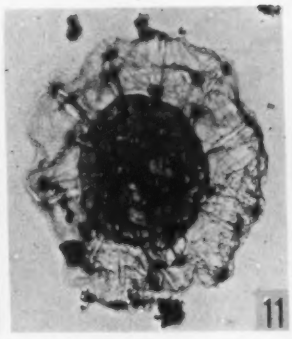
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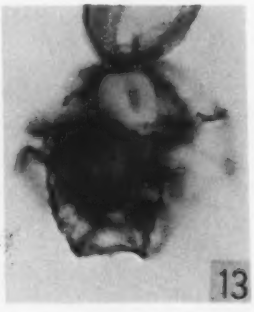
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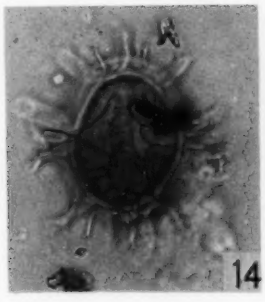
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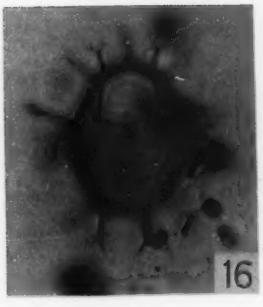
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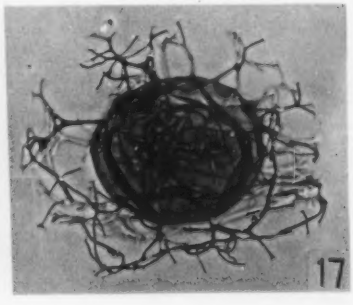
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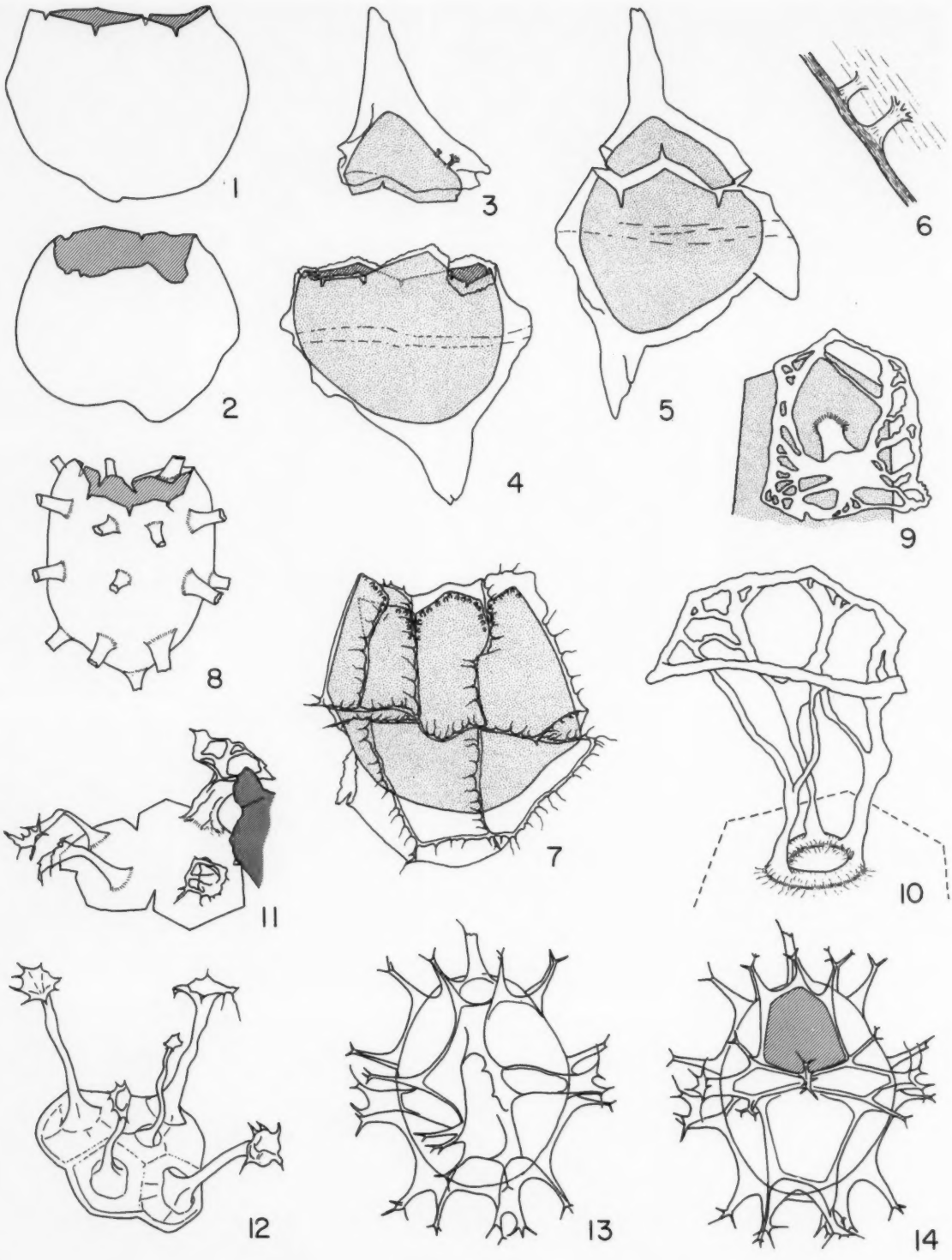
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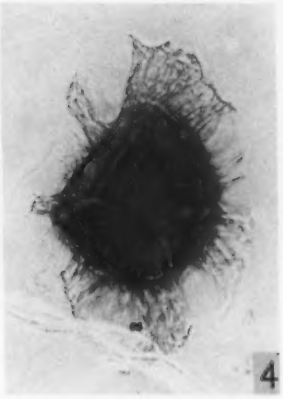
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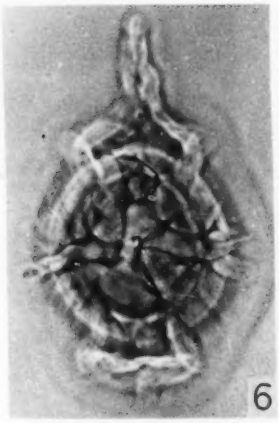
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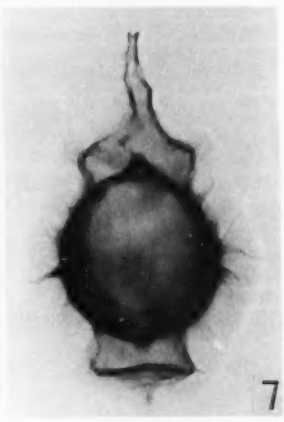
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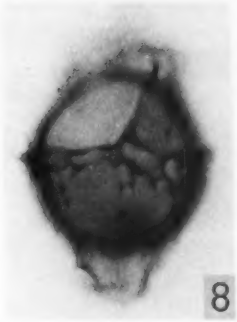
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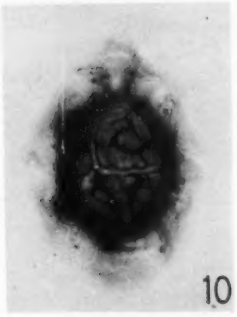
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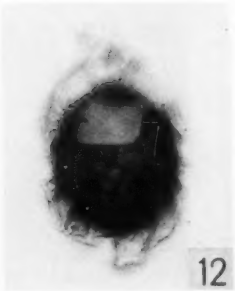
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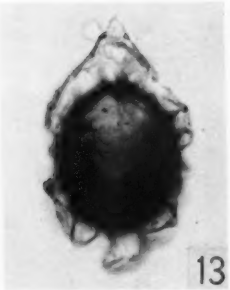
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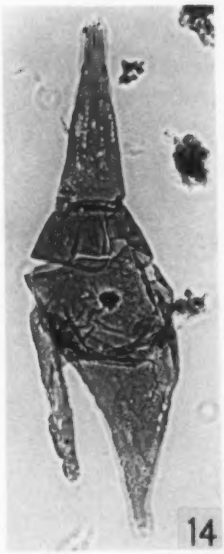
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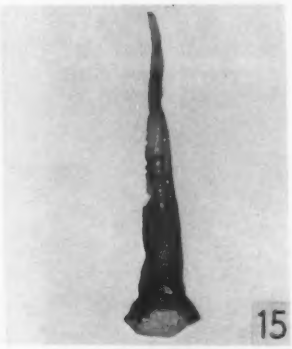
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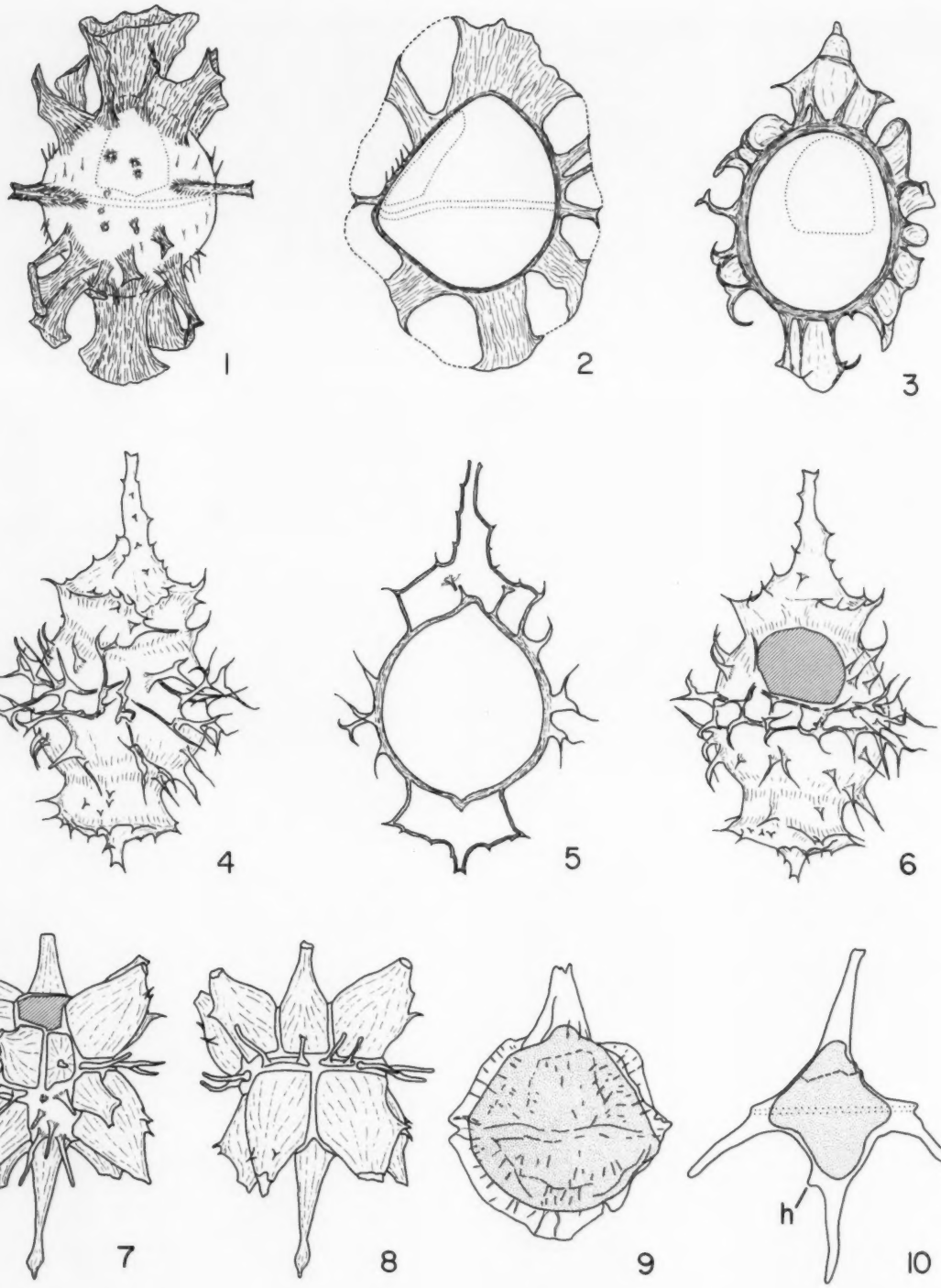
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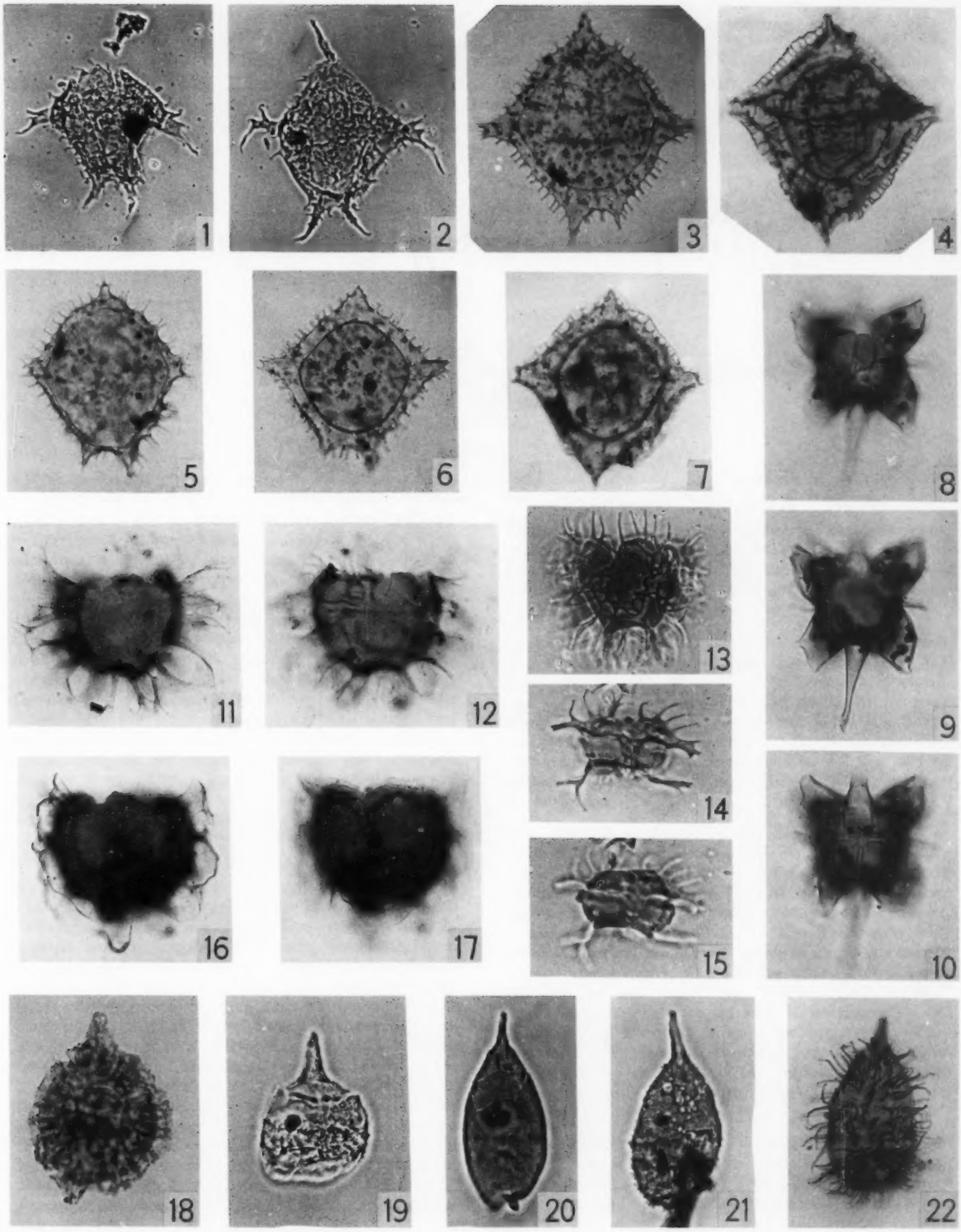
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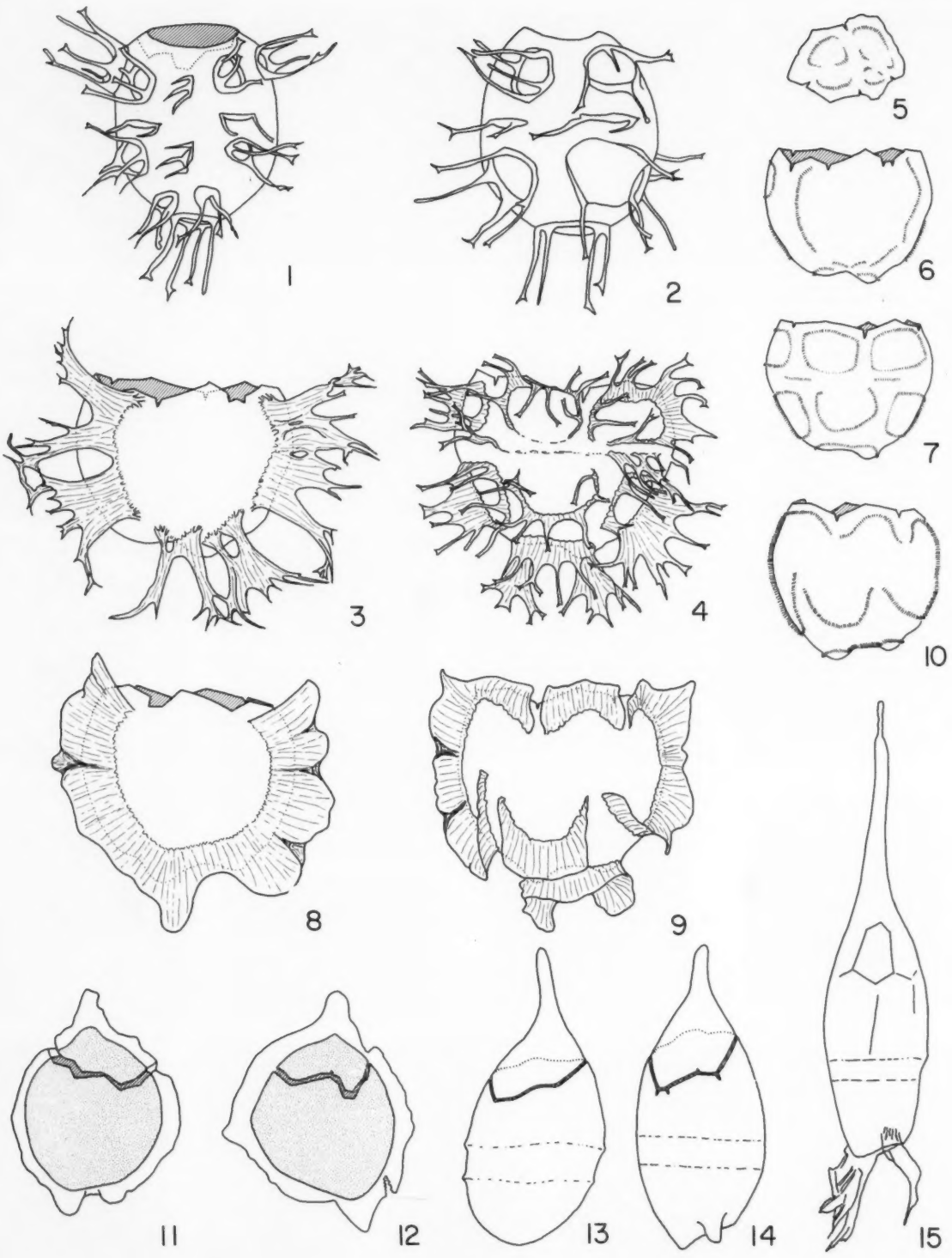
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ABSTRACT

The occurrence of Lepidocyclina *in the upper Eocene to the lower Miocene of the Indian region is discussed, and the validity of the subgenus* Trybliolepidina *is supported. Two new species,* Lepidocyclina (Trybliolepidina) kathiawarensis *Chatterji and* L. (T.) raoi *Chatterji, and one new variety,* L. (Nephrolepidina) martini *(Schlumberger) var.* kamalae *Chatterji, along with* L. (N.) morgani *(Lemoine and Douvillé) and* L. (N.) borneensis *(Provale), are described from the Gaj beds (lower Miocene) of Kathiawar, western India.*

The occurrence of Lepidocyclina in India

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Geological Survey of India
Calcutta, India

INTRODUCTION

The richly fossiliferous Miocene beds of Kathiawar have long been known to Indian geologists; Fedden (1884) was the first to give an account of them. Since Fedden's pioneer work, little was added to our knowledge until Mohan and Chatterji visited the area in 1952–54 and published (1956) a joint paper discussing the stratigraphy of these beds. Another paper dealing with the correlation of the Miocene beds of western India and Ceylon was published by Chatterji, S. R. N. Rao, *et al.* (1957). A systematic study of the genera *Austrotrillina*, *Operculina*, *Taberina*, *Archaias*, *Sorites*, *Borelis*, *Gypsina*, and *Lepidocyclina* occurring in the Gaj beds (lower Miocene) of Kathiawar has been carried out by the author; the present paper concerns the lepidocyclines only. In the synonymy lists, only the important references are given. The collections and all figured types, have been deposited in the Museum of the Geology Department, University of Lucknow.

LEPIDOCYCLINES IN THE INDIAN REGION

Lepidocyclina-bearing beds are quite widespread in India and adjacent countries. They have been reported in Burma, the Andaman Islands, Quilon, Surat-Broach, Kutch, Sind-Baluchistan (Pakistan), and lately from Kathiawar. As early as 1888, Carter reported the occurrence of *Lepidocyclina* in the lower Pegu limestones (upper Oligocene) of Burma, under the name *Orbitolites mantelli* var. *theobaldi* Carter. Vredenburg (1906) believed this form to be *L. (Eulepidina) elephantina* Munier-Chalmas. A second horizon in Burma is known as the "Yaw" stage (upper Eocene, Priabonian); Rao (1942*a*) described *L. (Polylepidina) birmanica* Rao, along with *Discocyclina*, *Asterophragmina*, and *Nummulites* from these beds. Rao (1946) re-examined the lepidocyclines of the lower Pegu series and recognized *L. (Eulepidina) theobaldi* (Carter), *L. (E.) dilatata* Michelotti, *L. (E.) formosa* Schlumberger, *L. (Nephrolepidina) sondaica* Yabe and Hanzawa, and *L. (N.) marginata* Michelotti, along with *Cycloclypeus*, *Amphistegina*, and *Heterostegina*.

Tipper (1911) and Gee (1926) reported the occurrence of *Lepidocyclina* in the Little Andaman Islands. Rao (1942*b*) held the opinion that the faunal assemblage resembled that of the lower Pegu of Burma, which would indicate a late Oligocene age.

Jacob and Sastri (1952) described lepidocyclines from well cores of Chavara, Quilon (Kerala), as *L. (N.) sumatrensis* (Brady), *L. (N.)* cf. *marginata* Michelotti, and *L. (N.) chavarana* Jacob and Sastri, along with many other forms. *L. (N.) chavarana* Jacob and Sastri was suspected by them to be a *Trybliolepidina*, but they preferred to place it in *Nephrolepidina*. To the present author it appears to be more like *Trybliolepidina* than *Nephrolepidina*.

The Tertiary exposures of the Surat-Broach area in western India were investigated by Rao (1941), who reported (1945) that these beds can be distinctly divided into two horizons: (1) The lower group, upper Eocene in age, characterized by the genera *Pellatispira*, *Discocyclina*, and *Nummulites*, for which Eames (1952) proposed the name "Tapti" series as a new horizon in Indian stratigraphy; and (2) the upper group, lower Miocene in age, called the "Agate conglomerates" and containing *Lepidocyclina* and *Miogypsina*. Rao and Singh (1956) re-examined them and reported *L. (N.) tournoueri* (Lemoine and Douvillé) and *L. (N.) sumatrensis* (Brady) var. *taptiensis* Rao and Singh, along with *Miogypsina* and *Austrotrillina;* they assigned a lower Miocene age to these beds.

Two *Lepidocyclina*-bearing sequences are known in Kutch; one is the lower Nari beds (lower Oligocene), from which *L. (Eulepidina) dilatata* Michelotti has been reported, and the second is the Gaj beds (lower

Miocene), from which *L. (N.) tournoueri* (Lemoine and Douvillé) and *L. (N.) sumatrensis* (Brady) were reported by Sah (1954).

Nuttall (1926) recognized two *Lepidocyclina* horizons in the Oligocene-Miocene beds of Mula Pass, Sind-Baluchistan border. From the Oligocene beds he described *L. (E.) dilatata* Michelotti, along with *Nummulites;* from the Miocene beds he recorded only one microspheric form, as *L. blanfordi* Nuttall.

Davis and Pinfold (1937) reported the occurrence of *L. (Polylepidina) punjabensis* Davies from the Ranikot beds (Paleocene) of the Salt Range (Pakistan), in association with *Nummulites*, *Assilina*, *Discocyclina*, and many other forms. This form was originally noted by Douvillé (1916) as *Lepidorbitoides tibetica* Douvillé from Kampa Dzong, Tibet. The original material was later studied by Rao (1940), who placed it under a new subgenus, *Orbitosiphon* Rao.

The author, along with Sah *et al.* (1953), reported the occurrence of *Lepidocyclina* in the Gaj beds (lower Miocene) of Kathiawar, when *Trybliolepidina* was noted for the first time in India. Three distinct sequences are now recognized here, as follows (in descending order):

3) "*Orbiculina*" limestones of Bhogat and Verawal, containing *L. (Trybliolepidina) kathiawarensis* n. sp., *L. (T.) raoi* n. sp., *L. (Nephrolepidina) martini* (Schlumberger) var. *kamalae* n. var., *L. (N.) borneensis* (Provale), and *L. (N.) morgani* (Lemoine and Douvillé), along with *Austrotrillina*, *Taberina*, and *Miogypsina*.

2) Visawara limestones of Visawara, containing *L. (N.) borneensis* (Provale,) *Austrotrillina*, and *Miogypsina*.

1) Bhatia limestones *(Miogypsina* beds) of Bhatia, containing only *Miogypsina*.

The age of these three units is clearly lower Miocene (Burdigalian); Unit 3 is upper Burdigalian, and Units 2 and 1 are lower Burdigalian. They correspond to stage f_1–f_2 of the "letter" classification of Indonesia.

From the preceding discussion it is apparent that *Polylepidina* occurs in the oldest Tertiary beds (Eocene, Priabonian) of the Indian region. This is followed by the lower Oligocene lower Nari beds of Sind-Baluchistan and Kutch, where the subgenus *Eulepidina* occurs alone. This stage is succeeded by the upper Oligocene of Burma and the Andaman Islands, where *Eulepidina* and *Nephrolepidina* occur together. The next stage is the lower Miocene (lower Burdigalian) of Surat-Broach, Visawara, and Kutch, where *Nephrolepidina* occurs alone. The youngest stage is represented in Kathiawar and Quilon, where the subgenera *Nephrolepidina* and *Trybliolepidina* occur together; these beds have been assigned to the upper Burdigalian stage, of lower Miocene age.

VALIDITY OF THE SUBGENUS TRYBLIOLEPIDINA VAN DER VLERK

The subgenus *Trybliolepidina* was introduced by I. M. van der Vlerk in 1928; since then there has been a difference of opinion about the validity of this subgenus. Caudri (1934), in her revision of the work of van der Vlerk, observed complete intergradation in a single species from the nephro- to the trybliolepidine type of embryonic apparatus. Prior to this, Gerth (1930) stated: "As species of *Lepidocyclina* which show a transition from the *Nephrolepidina*-stage to the *Trybliolepidina*-stage have already been found in the older Miocene, the occurrence of *Trybliolepidina* is not a true indication for the younger Miocene." Tan (1930) stated that the subgenus *Trybliolepidina* has no stratigraphic significance. Vaughan and Cole (in Cushman, 1950, p. 363) stated: "Since this intergradation may be demonstrated in a single species, it appears that the two subgenera should not be recognised." Hanzawa was also of the same opinion.

The author, while studying the association of *Nephrolepidina* and *Trybliolepidina* in Kathiawar, became convinced that the latter should be regarded as a valid subgenus. Here, *Trybliolepidina* has always been found to possess more nepionic chambers than *Nephrolepidina*. The number of nepionic chambers in *Nephrolepidina* is always four to six and never more than six, but in *Trybliolepidina* it always ranges from six to nine. Difficulty arises when there are six nepionic chambers present, but it can be resolved by studying the other characters carefully in the equatorial and vertical sections. The vertical sections of *Trybliolepidina* from Kathiawar show multiplication of the equatorial layer near the periphery of the radial ridges. In addition, *Nephrolepidina* is somewhat more primitive than *Trybliolepidina* in its evolutionary stage. In *Nephrolepidina*, the equatorial chambers may range from arcuate to hexagonal, but in *Trybliolepidina* the equatorial chambers are never arcuate and always range from ogival to hexagonal, spatulate, or hexagonal-spatulate in outline. The test in *Trybliolepidina* is mostly stellate, whereas in *Nephrolepidina* it is generally circular, although rarely it may also be stellate. Morphologically, there is little doubt that *Trybliolepidina* represents the highest evolutionary stage among the lepidocyclines. It has been generally observed that when *Trybliolepidina* occurs alone, it is mostly associated with younger strata than *Nephrolepidina*. Thus, it appears that *Trybliolepidina* is an end form of the nephrolepidine lineage.

The process of intergradation is not only a problem in *Nephrolepidina* and *Trybliolepidina* but is also met with in *Eulepidina* and *Nephrolepidina*. Furthermore, *Eulepidina* also intergrades with *Trybliolepidina*. Because of all these intergradations, Vaughan and Cole (in Cushman, 1950, p. 350) stated: "The initial chambers...have size relationship to each other varying from equality *(Lepidocyclina* s.s.) to the second chamber so large that it completely embraces the initial chamber *(Eulepidina)*. Within a single species intergradation of types may be found, and difficulty may be encountered in placing a specimen in a genus, or, particularly, in a subgenus."

TABLE 1

DISTRIBUTION OF LEPIDOCYCLINA AND OTHER FORAMINIFERA IN KATHIAWAR, WESTERN INDIA

Species \ Localities	Kathiawar			
	C	H	Vf	Vwl
Lepidocyclina (Nephrolepidina) borneensis (Provale)		×	×	
L. (N.) morgani (Lemoine and Douvillé)				×
L. (N.) martini (Schlumberger) var. *kamalae* Chatterji, n. var.		×		
L. (Trybliolepidina) kathiawarensis Chatterji, n. sp.		×		
L. (T.) raoi Chatterji, n. sp.				×
Miogypsina (Miogypsina) irregularis (Michelotti)			×	×
M. (M.) bhogatensis Mohan		×		
M. (Lepidosemicyclina) polymorpha (Rutten)		×		
M. (L.) thecideaeformis (Rutten)			×	
Austrotrillina howchini (Schlumberger)	×	×	×	×
Operculina bartschi Cushman				×
O. granulosa Leymerie				×
O. complanata (Defrance)				×
Taberina malabarica (Carter)	×	×		×
Archaias angulatus (Fichtel and Moll)				×
Sorites marginalis (Lamarck)				×
Borelis cf. *melo* (Fichtel and Moll)		×		
Gypsina globulus (Reuss)		×		×

Crespin (1943), in revising the lepidocyclines of Victoria, Australia, described as *Trybliolepidina* all the species that had previously been referred to *Nephrolepidina*. She was definitely of the opinion that *Trybliolepidina* and *Nephrolepidina* are distinct subgenera. She recognized the following characters as diagnostic in *Trybliolepidina* from Victoria:

1) Trybliolepidine type of embryonic apparatus in the megalospheric forms.

2) Two or three more nepionic chambers than *Nephrolepidina*, which has four to six nepionic chambers (two primary auxiliary and two, rarely more, ad-auxiliary chambers). Thus, in *Trybliolepidina* there are six to eight nepionic chambers (two primary auxiliary and four or more ad-auxiliary chambers).

3) The equatorial chambers in both the megalospheric and microspheric forms are chiefly ogival to spatulate in shape, but sometimes hexagonal ones are present in the rayed portion of the test.

Crespin was also of the opinion that the subgenus *Trybliolepidina* indicates a particular horizon in the Indo-Pacific region. Bronnimann (1946) also recognized *Trybliolepidina* as a valid subgenus, and described *L. (T.) renzi* (David-Sylvain) from Morocco, which lies outside the Indo-Pacific region.

One important character of *Trybliolepidina* which has not been observed by other workers is noted here for the first time. In the stellate part of the test of this subgenus in Kathiawar, as mentioned earlier, there are found several layers of equatorial chambers instead of a single layer as in *Nephrolepidina* and all other subgenera. This phenomenon is clearly demonstrated in the vertical sections of *L. (T.) kathiawarensis* Chatterji, which is associated with *L. (N.) martini* (Schlumberger) var. *kamalae* Chatterji in Kathiawar, in which only one layer of equatorial chambers is present (pl. 4, figs. 2–3, 9–10).

Plate 4, figure 3, shows a vertical section of *L. (T.) kathiawarensis* Chatterji passing through the center and cutting the stellate part of the test. It is interesting to note that, in this region, the equatorial chambers multiply and are three to four layers thick at the periphery, although the equatorial layer is single in other parts of the test. In *L. (N.) martini* (Schlumberger) var. *kamalae* Chatterji, which is also stellate and which Crespin (1943) and others regarded as a *Trybliolepidina*, the stellate parts are found to be made up of a single layer of equatorial chambers (pl. 4, fig. 9). For this reason, and also on account of the embryonic apparatus, this species is here considered to be a *Nephrolepidina*.

PROVENANCE OF MATERIAL

The samples for the present study were collected from four different localities in Kathiawar. The distribution of the genus *Lepidocyclina*, along with other foraminifera, is shown in Table 1. The family Miogypsinidae from Kathiawar has been described by Mohan (1958). The localities of the samples are as follows:

a) Bhogat area:
Bhatia village (69°16′E.; 22°06′N.); Loc. C (Bhatia): 1.5 miles NNE of Bhatia village.
Bhogat village (69°14′E.; 21°59′N.); Loc. H (Bhogat): 1.5 miles N. 34°E. from Bhogat village.
Visawara village (69°27′E.; 21°46′N.); Loc. Vf (Visawara): About 2.5 miles north of Visawara village.

b) Verawal area:
Khorasa village (70°22′E.; 22°03′N.); Loc. Vwl (Verawal): About 1.5 miles west of Khorasa village.

SYSTEMATIC DESCRIPTIONS

Order FORAMINIFERA
Family ORBITOIDIDAE Schubert, 1920
Subfamily LEPIDOCYCLININAE Tan, 1936
Genus LEPIDOCYCLINA Gümbel, 1870
Subgenus NEPHROLEPIDINA Douvillé, 1911

Lepidocyclina (Nephrolepidina) borneensis (Provale)

Plate 1, figures 1–6

Lepidocyclina tournoueri (Lemoine and Douvillé) var. *borneensis* PROVALE, 1909, Riv. Ital. Pal., vol. 15, pt. 2, p. 74.
Lepidocyclina (Nephrolepidina) tournoueri (Lemoine and Douvillé) var. *borneensis* (Provale). – DOUVILLÉ, 1911, Philippine Jour. Sci., vol. 6, p. 68.

TABLE 2

VARIATION IN EXTERNAL MEASUREMENTS

Lepidocyclina (Nephrolepidina) borneensis (Provale)

Specimen no.	Diameter of test (mm.)	Thickness of test (mm.)	Diameter of central boss (mm.)
1	1.97	0.97	1.02
2	3.70	0.92	1.82
3	3.77	1.40	2.52
4	4.52	1.87	2.17
5	4.77	1.40	1.22

TABLE 3

MEASUREMENTS OF MEDIAN SECTIONS

Lepidocyclina (Nephrolepidina) borneensis (Provale)

Dimensions	Specimen number				
	6	7	8	9	10
Diameter of test (in mm.)	3.85	2.75	3.85	4.30	3.75
Thickness of test (in mm.)	1.42	1.00	1.17	1.60	1.00
Ratio of D/T	2.7	2.7	3.2	2.6	3.7
Embryonic chambers:					
Diameter of protoconch	141.9μ	141.9μ	236.5μ	223.6μ	253.7μ
Diameter of deuteroconch	240.6μ	219.3μ	335.4μ	339.7μ	344.0μ
Ratio of D/P	1.6	1.5	1.4	1.5	1.3
Distance across both chambers	223.6μ	202.1μ	318.2μ	318.2μ	313.9μ
Thickness of partition wall	8.6μ	12.9μ	12.9μ	12.9μ	12.9μ
Thickness of outer wall	12.9μ	17.2μ	17.2μ	21.5μ	17.2μ
Equatorial chambers:					
Near center:					
Radial diameter	47.3μ	47.3μ	47.3μ	43.0μ	47.3μ
Tangential diameter	43.0μ	47.3μ	47.3μ	43.0μ	47.3μ
Near periphery:					
Radial diameter	55.9μ	43.0μ	43.0μ	43.0μ	43.0μ
Tangential diameter	55.9μ	47.3μ	47.3μ	51.6μ	47.3μ

TABLE 4

MEASUREMENTS OF VERTICAL SECTIONS

Lepidocyclina (Nephrolepidina) borneensis (Provale)

Dimensions	Specimen number				
	11	12	13	14	15
Diameter of test (in mm.)	4.52	4.50	3.50	3.77	3.70
Thickness of test (in mm.)	1.87	1.85	1.30	1.40	0.92
Ratio of D/T	2.4	2.4	2.6	2.6	3.0
Diameter of central boss (in mm.)	2.17	2.15	1.87	1.52	1.82
Width of flange (in mm.)	2.35	2.34	1.42	1.25	1.87
Thickness of flange	189.2μ	193.5μ	172.0μ	86.0μ	150.5μ
Embryonic chambers:					
Length	249.4μ	215.0μ	296.7μ	245.1μ	279.5μ
Height	172.0μ	172.0μ	202.1μ	167.7μ	180.6μ
Thickness of outer wall	25.8μ	25.8μ	25.8μ	21.5μ	21.5μ
Lateral chambers:					
Number of tiers on each side of embryonic apparatus	17	16	14	13	11
Length	120.4μ	129.0μ	150.5μ	219.3μ	236.5μ
Height	25.8μ	25.8μ	34.4μ	38.7μ	47.3μ
Thickness of floors and roofs	12.9μ	12.9μ	12.9μ	17.2μ	17.2μ
Surface diameter of pustules	258.0μ	215.0μ	215.0μ	258.0μ	258.0μ

Lepidocyclina (Amphilepidina) borneensis (Provale). – Douvillé, 1925, Soc. Géol. France, Mém., new ser., vol. 1, no. 2.
Lepidocyclina (Nephrolepidina) borneensis (Provale). – van der Vlerk, 1928, Eclogae Geol. Helv., vol. 21, no. 1, p. 192. – Scheffen, 1932, Wetensch. Meded., no. 21. – Mohler, 1946, Eclogae Geol. Helv., vol. 39, p. 302.

Material: Loc. H (Bhogat): "Form A" – Nineteen specimens measured externally, ten studied in median section, and five in vertical section; "Form B" – Five specimens measured externally and three studied in median section. – Loc. Vf (Visawara): "Form A" – Twenty specimens measured externally, fourteen studied in median section, and six in vertical section; "Form B" – Three specimens measured externally and two studied in median section.

"Form A"

External characters: Test lenticular; circular in outline, with a narrow, thin flange and a well-developed central boss, with one centrally placed pustule or with four or five pustules surrounding the centrally placed one. Diameter of test 1.97–4.77 mm.; thickness 0.92–1.87 mm.; diameter of central boss 1.02–2.52 mm.

Internal characters – median section: The embryonic apparatus is bilocular and of typical nephrolepidine type; the deuteroconch partially embraces the protoconch and is reniform in shape; the outer wall of the embryonic apparatus is of normal thickness, ranging from 12.9μ to 21.5μ; the diameter of the protoconch varies from 141.9μ to 253.7μ and that of the deuteroconch from 219.3μ to 344.0μ; the length across both chambers varies from 202.1μ to 318.2μ, and the thickness of the partition wall between the protoconch and the deuteroconch from 8.6μ to 12.9μ. The number of nepionic chambers is fairly constant, generally four to six, consisting of two primary auxiliary and three to four ad-auxiliary chambers.

The equatorial layer is nonpolygonal, with the chambers arranged in concentric rings. The chambers are fairly uniform in size from the earlier to the later ontogenetic stages; they are hexagonal at the center and tend to become spatulate near the periphery; the chambers are 43.0μ by 43.0μ.

Internal characters – vertical section: Test biconvex, equatorial layer conspicuous and narrow at the center, gradually enlarging toward the periphery, where it occupies the complete thickness of the test. The lateral chambers are elongate and arranged in regular tiers, numbering 14 to 17 on each side of the equatorial layer; the length of the lateral chambers varies from 120.4μ to 236.5μ, the height from 25.8μ to 47.3μ, and the thickness of the wall between two chambers from 12.9μ to 17.2μ; generally there is only one pillar, but in a few cases there are 4 or 5 pillars present; their surface diameter is about 258.0μ.

"Form B"

External characters: Test lenticular, circular in outline, with a well-developed central boss, usually with one centrally placed pustule but in a few cases with many pustules scattered over the whole surface; diameter of test 6.02–8.75 mm.; thickness 2.30–2.75 mm.; diameter of central boss 3.77–4.17 mm.

Internal characters – median section: The nucleoconch is microspheric and planispiral; the equatorial chambers are arranged in concentric rings and are usually hexagonal in shape with negligible variation in size; near the periphery they are sometimes spatulate to hexagonal spatulate in shape.

Observations and discussion: The present form from Kathiawar is identical with *L. (N.) borneensis* (Provale,) which, according to Crespin (1943), appears to be the Indo-Pacific representative of *L. (N.) tournoueri* (Lemoine and Douvillé). That form also has a nonpolygonal equatorial layer, composed predominantly of hexagonal equatorial chambers.

Distribution: Found at localities H (Bhogat) and Vf (Visawara) in Kathiawar.
Age: Burdigalian.

Lepidocyclina (Nephrolepidina) martini (Schlumberger) var. kamalae Chatterji, new variety

Plate 1, figures 7–10; plate 2, figures 1–4; plate 4, figures 9–10

Holotype: Specimen shown in plate 2, figure 2.

Material: "Form A" – Forty specimens measured externally, thirty studied in median section, and ten in vertical section; "Form B" – Five specimens measured externally and five studied in median section.

"Form A"

External characters: Test lenticular, stellate, flat, with a prominent central boss and a thin peripheral flange, which is star-shaped, with six to eight or nine rays; the periphery of the rays is thick; except for a single pustule on the center of the test, the surface is smooth; diameter of test 2.75–4.20 mm.; thickness 1.25–1.75 mm.; diameter of central boss 1.57–2.60 mm.

Internal characters –median section: The embryonic apparatus is bilocular and of typical nephrolepidine type, with a thick outer wall, varying in thickness from 12.9μ to 21.5μ; the deuteroconch partially embraces the protoconch; the diameter of the protoconch varies from 133.9μ to 202.1μ and that of the deuteroconch from 206.4μ to 288.1μ; the length across both chambers varies from 189.2μ to 296.7μ, and the thickness of the partition wall between the protoconch and the deuteroconch from 8.6μ to 17.2μ; there are four to six nepionic chambers, two primary auxiliary and two to four ad-auxiliary chambers.

TABLE 5

VARIATION IN EXTERNAL MEASUREMENTS

Lepidocyclina (Nephrolepidina) martini (Schlumberger) var. *kamalae* Chatterji, n. var.

Specimen no.	Diameter of test (mm.)	Thickness of test (mm.)	Diameter of central boss (mm.)
1	2.75	1.25	1.57
2	3.72	1.47	2.60
3	3.77	1.35	1.62
4	4.12	1.42	2.42
5	4.20	1.75	2.17

TABLE 6

MEASUREMENTS OF MEDIAN SECTIONS

Lepidocyclina (Nephrolepidina) martini (Schlumberger) var. *kamalae* Chatterji, n. var.

Dimensions	Specimen number				
	6	7	8	9	10
Diameter of test (in mm.)	3.72	4.20	4.12	3.77	3.67
Thickness of test (in mm.)	1.47	1.75	1.42	1.62	1.37
Ratio of D/T	2.3	2.9	2.8	2.9	2.6
Embryonic chambers:					
Diameter of protoconch	133.9μ	189.2μ	180.6μ	176.3μ	202.1μ
Diameter of deuteroconch	206.4μ	296.7μ	258.0μ	249.4μ	288.1μ
Ratio of D/T	1.5	1.5	1.4	1.4	1.4
Distance across both chambers	189.2μ	296.7μ	262.3μ	249.4μ	275.2μ
Thickness of partition wall	12.9μ	17.2μ	8.6μ	12.9μ	12.9μ
Thickness of outer wall	17.2μ	21.5μ	17.2μ	17.2μ	21.5μ
Equatorial chambers:					
Near center:					
Radial diameter	38.7μ	47.3μ	43.0μ	51.6μ	43.0μ
Tangential diameter	34.4μ	43.0μ	43.0μ	43.0μ	43.0μ
Near periphery:					
Radial diameter	47.3μ	64.5μ	64.5μ	68.8μ	64.5μ
Tangential diameter	38.7μ	55.9μ	55.9μ	60.2μ	55.9μ

TABLE 7

MEASUREMENTS OF VERTICAL SECTIONS

Lepidocyclina (Nephrolepidina) martini (Schlumberger) var. *kamalae* Chatterji, n. var.

Dimensions	Specimen number				
	11	12	13	14	15
Diameter of test (in mm.)	3.25	3.42	3.87	3.25	3.37
Thickness of test (in mm.)	1.30	1.52	1.55	1.25	1.42
Ratio of D/T	2.5	2.2	2.5	2.6	2.3
Diameter of central boss (in mm.)	2.00	2.02	2.12	2.02	2.15
Width of flange (in mm.)	1.25	1.40	1.75	1.12	1.22
Thickness of flange	374.1μ	137.6μ	236.5μ	253.7μ	227.9μ
Embryonic chambers:					
Length	219.3μ	180.6μ	283.8μ	172.0μ	258.0μ
Height	141.9μ	133.9μ	180.6μ	167.7μ	150.5μ
Thickness of outer wall	17.2μ	17.2μ	21.5μ	17.2μ	17.2μ
Lateral chambers:					
Number of tiers on each side of embryonic apparatus	15	13	13	15	14
Length	111.8μ	154.8μ	137.6μ	150.5μ	129.0μ
Height	34.4μ	43.0μ	43.0μ	43.2μ	43.0μ
Thickness of floors and roofs	17.2μ	17.2μ	12.9μ	17.2μ	17.2μ
Surface diameter of pustules	277.5μ	344.0μ	258.0μ	322.5μ	270.9μ

The equatorial layer is polygonal, with four to six rays commencing from the center; in the rayed portion the chambers are larger and are ogival in shape, but between the rays they are hexagonal at the center, rapidly becoming spatulate-hexagonal near the periphery; the chambers are, however, variable in shape and size; at the center they are 51.6μ by 43.0μ, but near the periphery they are 68.8μ by 60.2μ.

Internal characters – vertical section: Test biconvex, with a prominent equatorial layer which increases in height at the periphery, where it occupies nearly the entire thickness of the test. The lateral chambers are elongate and are arranged in regular tiers; there are 13 to 15 tiers on each side of the equatorial layer; the length of the chambers varies from, 11.8μ to 154.8μ, the height from 34.4μ to 43.0μ, and the thickness of the wall between chambers from 12.9μ to 17.2μ.

"Form B"

External characters: Test lenticular, stellate, with a prominent central boss and six to nine protruding rays; surface smooth, with about six pustules on the central boss; in a few forms there is only one centrally placed pustule; diameter of test 3.80–8.95 mm.; thickness 2.30–2.95 mm.; diameter of central boss 2.70–3.67 mm.

Internal characters – median section: The nucleoconch is microspheric, planispiral; the equatorial layer is polygonal, with four to six rays; in the rayed portion the chambers are ogival, but between the rays they are hexagonal to spatulate-hexagonal in shape; the chambers vary greatly in shape and size.

Observations and discussion: The present form from Kathiawar closely resembles *L. (N.) martini* (Schlumberger), differing from it mainly in the shape of the equatorial chambers; thus a new variety is here proposed as *L. (N.) martini* (Schlumberger) var. *kamalae* n. var. The equatorial chambers of *L. (N.) martini*, according to Cole (1945), are arcuate at the center but rapidly become spatulate, and near the periphery they are elongate-spatulate. In the present form, the equatorial chambers are ogival to spatulate at the center but spatulate-hexagonal at the periphery. Except for this marked difference, these two forms are almost alike in the arrangement of the equatorial chambers, the lateral layers, and the shape of the test.

There seems to be a controversy about this species. Originally it was described by Schlumberger (1900) from Batoo, Koetjing, Madoera, as *Lepidocyclina martini*. Later, van der Vlerk (1928) placed it in the subgenus *Nephrolepidina*. Crespin (1943) and Mohler (1946) regarded it as a *Trybliolepidina*. Cole (1945) considered it to be a *Nephrolepidina* and commented: "The embryonic apparatus varies from nephrolepidine to trybliolepidine." Mohler (1946) recorded it from the Burdigalian of Borneo in association with *L. (N.) borneensis* (Provale), *Miogypsina*, *Austrotrillina*, *Amphistegina*, *Archaias*, *Gypsina*, and many other forms. This assemblage is strikingly similar to that of Kathiawar. Here, in addition to the forms listed above, the present form is also associated with *L. (Trybliolepidina) kathiawarensis* Chatterji, n. sp., which is differentiated from the present form as indicated below; hence the present species is here regarded as a *Nephrolepidina*.

L. (N.) martini var. *kamalae*	*L. (T.) kathiawarensis*
Stellate form with no radial ridges.	Stellate form with radial ridges.
No multiplication of the equatorial layer.	Definite multiplication of the equatorial layer near the periphery of the stellate part of the test.
Nephrolepidine type of embryonic apparatus.	Trybliolepidine type of embryonic apparatus.
Less than six periembryonic chambers.	More than six periembryonic chambers.
Equatorial chambers hexagonal to ogival or spatulate-hexagonal in shape.	Dominance of ogival and spatulate equatorial chambers; hexagonal chambers absent.

Type locality: Found only at locality H (Bhogat) in Kathiawar.

Age: Burdigalian.

Lepidocyclina (Nephrolepidina) morgani
(Lemoine and Douvillé)
Plate 2, figures 5–8

Lepidocyclina morgani LEMOINE and DOUVILLÉ, 1904, Soc. Géol. France, Mém. vol. 12, no. 32, p. 17.

Lepidocyclina (Nephrolepidina) morgani (Lemoine and Douvillé). – VAUGHAN, 1924, Geol. Soc. Amer., Bull., vol. 35, p. 798. – DOUVILLÉ, 1925, Soc. Géol. France, Mém., new ser., vol. 2, fasc. 2, p. 80. – YABE and HANZAWA, 1926, Tôhoku Imp. Univ., Sci. Repts., ser. 2 (Geol.), vol. 9, pp. 4–5, pl. 1, fig. 6. – VAN DER VLERK, 1928, Eclogae Geol. Helv., vol. 21, p. 8. – SILVESTRI, 1937, Palaeontogr. Ital., vol. 32, Suppl. 2, pp. 168–70, pl. 13, figs. 4–5.

Material: "Form A" – Twelve specimens measured externally, five studied in median section, and three in vertical section; "Form B" of this species has not been encountered.

"Form A"

External characters: This is a very small species of *Lepidocyclina* with a lenticular test, circular in outline, and with a well-developed central boss; the peripheral

TABLE 8

VARIATION OF EXTERNAL MEASUREMENTS

Lepidocyclina (Nephrolepidina) morgani
(Lemoine and Douvillé)

Specimen no.	Diameter of test (mm.)	Thickness of test (mm.)	Diameter of central boss (mm.)
1	1.52	0.65	1.02
2	1.80	1.00	1.56
3	2.17	1.25	1.92
4	2.80	1.60	2.17
5	2.80	1.75	2.17

TABLE 9

MEASUREMENTS OF MEDIAN SECTIONS

Lepidocyclina (Nephrolepidina) morgani (Lemoine and Douvillé)

Dimensions	Specimen number				
	6	7	8	9	10
Diameter of test (in mm.)	1.75	1.60	2.17	2.57	2.77
Thickness of test (in mm.)	0.65	1.00	1.25	1.27	1.52
Ratio of D/T	2.7	1.6	1.7	2.0	1.8
Embryonic chambers:					
Diameter of protoconch	133.9μ	150.5μ	184.9μ	202.1μ	193.5μ
Diameter of deuteroconch	197.8μ	193.5μ	206.4μ	296.7μ	215.0μ
Ratio of D/P	1.4	1.2	1.1	1.4	1.1
Distance across both chambers	193.5μ	172.0μ	189.2μ	288.1μ	197.8μ
Thickness of partition wall	17.2μ	21.5μ	17.2μ	21.5μ	17.2μ
Thickness of outer wall	25.8μ	25.8μ	25.8μ	30.1μ	25.8μ
Equatorial chambers:					
Near center:					
Radial diameter	43.0μ	43.0μ	43.0μ	38.7μ	43.0μ
Tangential diameter	43.0μ	43.0μ	43.0μ	43.0μ	43.0μ
Near periphery:					
Radial diameter	47.3μ	43.0μ	47.0μ	43.0μ	43.0μ
Tangential diameter	47.3μ	43.0μ	47.3μ	43.0μ	43.0μ

TABLE 10

MEASUREMENTS OF VERTICAL SECTIONS

Lepidocyclina (Nephrolepidina) morgani (Lemoine and Douvillé)

Dimensions	Specimen number		
	11	12	13
Diameter of test (in mm.)	1.52	1.77	1.80
Thickness of test (in mm.)	0.65	0.65	1.00
Ratio of D/T	2.3	2.7	1.8
Diameter of central boss (in mm.)	1.02	1.52	1.56
Width of flange (in mm.)	0.50	0.25	0.23
Thickness of flange	73.1μ	86.0μ	75.4μ
Embryonic chambers:			
Length	258.0μ	240.8μ	266.6 μ
Height	177.0μ	159.1μ	184.9μ
Thickness of outer wall	25.8μ	25.8μ	25.8μ
Lateral chambers:			
Number of tiers on each side of embryonic apparatus	10	10	13
Length	64.5μ	75.4μ	81.7μ
Height	25.8μ	25.8μ	25.8μ
Thickness of floors and roofs	17.2μ	17.2μ	17.2μ
Surface diameter of pustules	375.5μ	365.5μ	375.5μ

flange is narrow and thin and surrounds the central boss like a collar; the surface is covered with a network of numerous large pustules; the diameter of the test varies from 1.52 mm. to 2.80 mm., the thickness from 0.65 mm. to 1.75 mm., and the diameter of the central boss from 1.02 mm. to 2.17 mm.

Internal characters – median section: The embryonic apparatus is bilocular and of typical nephrolepidine type; the deuteroconch partially embraces the protoconch, which is reniform in shape; the outer wall of the embryonic apparatus is of normal thickness and varies from 25.8μ to 30.1μ; the diameter of the protoconch varies from 133.9μ to 202.1μ and that of the deuteroconch from 193.5μ to 296.7μ; the length across both chambers varies from 172.0μ to 288.1μ, and the thickness of the partition wall between the protoconch and the deuteroconch from 17.2μ to 21.5μ; the number of nepionic chambers is fairly constant, four to six, consisting of two primary auxiliary and two to four ad-auxiliary chambers.

The equatorial layer is nonpolygonal, with the chambers arranged in concentric rings; they are mostly uniform in shape and size; they are hexagonal at the center and tend to become elongate-hexagonal near the periphery; the size of the chambers is 43.0μ by 43.0μ.

Internal characters – vertical section: Test biconvex, with a conspicuous equatorial layer having a uniform height throughout; in a few specimens the height increases slightly near the periphery. The lateral chambers are arranged in regular tiers, numbering 10 to 13 on each side of the equatorial layer; the length of the lateral chambers varies from 64.5μ to 81.7μ; the height is about 25.8μ; and the thickness of the chamber walls is about 17.2μ; a large number of pillars are present, which protrude on the surface as pustules; their surface diameter is about 325.5μ.

Observations and discussion: The present form from Kathiawar is identical with *L. (N.) morgani* (Lemoine and Douvillé), which was first described from the Miocene (Burdigalian) of Andalusia, Spain. Later, it was also reported from the Miocene of Madagascar. This form differs from *L. (N.) tournoueri* (Lemoine and Douvillé) in having a large number of pustules and also in the shape of the equatorial chambers. In *L. (N.) tournoueri*, the equatorial chambers are mostly lozenge-shaped, whereas here they are hexagonal and elongate-hexagonal. The present form also differs from *L. (N.) borneensis* (Provale) in the shape of the equatorial chambers, which in that form are spatulate at the periphery and hexagonal at the center. These two forms also differ in the size and ornamentation of the test.

Distribution: Found only at locality Vwl (Verawal) in Kathiawar.

Age: Burdigalian.

Subgenus TRYBLIOLEPIDINA van der Vlerk, 1928

Lepidocyclina (Trybliolepidina) kathiawarensis Chatterji, **new species**
Plate 2, figure 9; plate 3, figures 1–8; plate 4, figures 1–3

Holotype: Specimen shown in plate 3, figure 4.

Material: "Form A" — Forty specimens measured externally, thirteen specimens studied in median section, and six in vertical section; "Form B" – Five specimens measured externally and five studied in median section.

"Form A"

External characters: Test lenticular, stellate, with a prominent central boss and a thin peripheral flange, which is star-shaped, with six to nine protruding rays; protuberances thick; surface reticulate, with prominent ridges running radially from the central boss to the end of the protuberances; diameter of test 2.42–4.22 mm.; thickness 0.97–1.85 mm.; diameter of central boss 1.35–2.35 mm.

Internal characters – median section: The embryonic apparatus is bilocular and of typical trybliolepidine type, with a thick outer wall; the protoconch is surrounded on three sides by the deuteroconch; the deuteroconch wall is at right angles to the protoconch; the diameter of the protoconch varies from 129.0μ to 219.3μ and that of the deuteroconch from 215.0μ to 331.1μ; the length across both chambers varies from 206.4μ to 296.7μ, the thickness of the outer wall from 12.9μ to 21.5μ, and the thickness of the partition wall between the protoconch and the deuteroconch from 8.6μ to 12.9μ; the number of nepionic chambers is fairly constant, six to nine, consisting of two primary auxiliary and four to seven ad-auxiliary chambers.

The equatorial layer is polygonal, with six to nine rays commencing from the center of the test; in the rayed portion the chambers are ogival at the center and spatulate to hexagonal-spatulate near the periphery; the rays are narrow near the center but broaden out at the periphery; the chambers between the rays are predominantly ogival in shape; the equatorial layer is undulant. The equatorial chambers are smaller at the center but enlarge at the periphery; at the center they are 47.3μ by 51.6μ, but near the periphery they are 60.2μ by 55.9μ.

Internal characters – vertical section: Test biconvex, with a conspicuous equatorial layer, which is narrow at the center and broadens out at the periphery, where it completely occupies the thickness of the test; the equatorial chambers are single-layered in the earlier ontogenetic stages, but two to three or even four layers are seen in the later stages in the stellate part of the test; this subdivision of the equatorial layer is well illustrated in plate 4, figure 3; compare this figure with *L. (N.) martini* (Schlumberger) var. *kamalae* Chatterji (pl. 4, figs. 9–10), where the equatorial layer also in-

TABLE 11

VARIATION IN EXTERNAL MEASUREMENTS

Lepidocyclina (Trybliolepidina) kathiawarensis Chatterji, n. sp.

Specimen no.	Diameter of test (mm.)	Thickness of test (mm.)	Diameter of central boss (mm.)
1	2.42	1.30	1.60
2	2.12	0.97	1.35
3	4.05	1.47	2.35
4	3.95	1.47	2.05
5	4.22	1.85	2.12

TABLE 12

MEASUREMENTS OF MEDIAN SECTIONS

Lepidocyclina (Trybliolepidina) kathiawarensis Chatterji, n. sp.

Dimensions	Specimen number				
	6	7	8	9	10
Diameter of test (in mm.)	3.42	3.55	3.25	2.12	4.22
Thickness of test (in mm.)	1.57	1.60	1.35	0.97	1.85
Ratio of D/T	2.1	2.2	2.4	2.1	2.8
Embryonic chambers:					
Diameter of protoconch	129.0μ	159.1μ	193.5μ	172.0μ	219.3μ
Diameter of deuteroconch	215.0μ	262.3μ	283.8μ	331.1μ	301.0μ
Ratio of D/P	1.6	1.6	1.4	1.9	1.3
Distance across both chambers	206.4μ	245.1μ	288.1μ	296.7μ	249.4μ
Thickness of partition wall	8.6μ	12.9μ	12.9μ	12.9μ	12.9μ
Thickness of outer wall	12.9μ	21.5μ	17.2μ	21.5μ	17.2μ
Equatorial chambers:					
Near center:					
Radial diameter	51.6μ	51.6μ	47.3μ	47.3μ	51.6μ
Tangential diameter	47.3μ	55.9μ	51.6μ	43.0μ	47.3μ
Near periphery:					
Radial diameter	60.2μ	43.0μ	51.6μ	51.6μ	47.3μ
Tangential diameter	55.9μ	43.0μ	47.3μ	47.3μ	43.0μ

TABLE 13

MEASUREMENTS OF VERTICAL SECTIONS

Lepidocyclina (Trybliolepidina) kathiawarensis Chatterji, n. sp.

Dimensions	Specimen number				
	11	12	13	14	15
Diameter of test (in mm.)	3.97	3.64	3.85	3.97	4.60
Thickness of test (in mm.)	1.40	1.47	1.47	1.27	1.35
Ratio of D/T	2.8	2.4	2.5	3.1	3.4
Diameter of central boss (in mm.)	2.37	2.20	2.15	2.22	2.65
Width of flange (in mm.)	1.60	1.44	1.70	1.75	1.95
Thickness of flange	387.0μ	344.0μ	288.1μ	249.4μ	236.5μ
Embryonic chambers:					
Length	253.7μ	258.0μ	236.5μ	215.0μ	215.0μ
Height	146.2μ	150.5μ	150.5μ	141.9μ	141.9μ
Thickness of outer wall	21.5μ	21.5μ	21.5μ	21.5μ	25.8μ
Lateral chambers:					
Number of tiers on each side of embryonic apparatus	13	14	14	17	17
Length	154.8μ	129.0μ	139.6μ	120.4μ	137.6μ
Height	34.4μ	34.4μ	34.4μ	25.8μ	34.4μ
Thickness of floors and roofs	12.9μ	12.9μ	12.9μ	12.9μ	12.9μ

creases in height toward the periphery but does not show subdivision into several layers.

The lateral chambers are elongate and are arranged in regular tiers; there are 13 to 17 tiers on each side of the equatorial layer; the length of the chambers varies from 90.3μ to 154.8μ and the height from 25.8μ to 34.4μ.

"Form B"

External characters: Test lenticular, stellate, with six to nine protruding rays; protuberances not generally visible, as all the specimens obtained were broken; surface of test reticulate, with six to eight pustules present; diameter of test 5.97–6.98 mm.; thickness 2.52–2.98 mm.; diameter of central boss 3.22–3.55 mm.

Internal characters – median section: The nucleoconch is microspheric and planispiral; the equatorial layer is polygonal, with six to nine rays; in the rayed part the chambers are ogival near the center and spatulate to hexagonal-spatulate near the periphery; the rest of the chambers are ogival in shape.

Observations and discussion: The present form from Kathiawar does not resemble any described form. The nearest approach is to *L. (T.) gippslandica* Crespin, in which the equatorial layer is polygonal with the chambers chiefly elongate-spatulate and rarely hexagonal in the rayed part, and ranging from ogival to spatulate in shape between the rays. In the present form, the equatorial layer is also polygonal, but the chambers are spatulate to hexagonal-spatulate near the periphery and ogival at the center in the rayed part, and ogival in shape between the rays. In addition, these two forms also differ in ornamentation, and they differ distinctly in the number of lateral layers. Thus, a new species, *Lepidocyclina (Trybliolepidina) kathiawarensis*, after the province of Kathiawar, where it occurs, is proposed for the present form.

Type locality: Found only at locality H (Bhogat village) in Kathiawar.

Age: Upper Burdigalian.

Lepidocyclina (Trybliolepidina) raoi
Chatterji, new species
Plate 4, figures 4–8

Holotype: Specimen shown in plate 4, figure 7.

Material: "Form A" – Ten specimens measured externally, four studied in median section, and two in vertical section; "Form B" of this species has not been encountered.

"Form A"

External characters: Test lenticular; surface smooth, with a few small pustules; test wavy in outline, with a narrow peripheral flange; diameter of test 2.20–3.80 mm.; thickness 0.87–1.25 mm.; diameter of central boss 1.35–2.42 mm.

Internal characters – median section: The embryonic apparatus is bilocular and of typical trybliolepidine type, with the outer wall moderately thick, ranging from 17.2μ to 21.5μ; the protoconch is surrounded on three sides by the deuteroconch; the diameter of the protoconch varies from 266.6μ to 292.4μ and of the deuteroconch from 489.1μ to 559.0μ; the distance across both chambers varies from 425.7μ to 451.5μ; the thickness of the partition wall between the protoconch and the deuteroconch is about 21.5μ; the number of nepionic chambers is fairly constantly eight or nine, consisting of two primary auxiliary and six to seven ad-auxiliary chambers. The equatorial layer is polygonal; all the chambers are ogival at the center and tend to become spatulate near the periphery; the chambers are 75.4μ by 60.2μ.

Internal characters – vertical section: Test biconvex, equatorial layer conspicuous, of uniform height throughout; the lateral chambers are arranged in regular tiers; there are 12 to 15 tiers on each side of the equatorial layer; the length of the chambers is about 111.8μ, and the height is about 34.4μ; there are numerous pillars present, but very few protrude as pustules.

Observations and discussion: The present form differs distinctly from *L. (T.) kathiawarensis* Chatterji in the absence of strongly developed rays and also in the characteristic shape of the embryonic apparatus. In the present form the equatorial chambers are ogival at the center and become spatulate near the periphery, but in *L. (T.) kathiawarensis* the chambers are ogival between the rays and ogival to spatulate or hexagonal-spatulate in the rayed portion. The present form has some similarity to *L. (T.) orientalis* van der Vlerk but differs from it distinctly in the shape of the equatorial chambers and embryonic apparatus. In *L. (T.) orientalis* van der Vlerk, the chambers are typically hexagonal. The present form from Kathiawar could not be identified with any described form; hence, the new species *Lepidocyclina (Trybliolepidina) raoi* is proposed here in honor of the late Professor S. R. N. Rao, of Lucknow University.

Type locality: Found only at locality Vwl (Verawal) in Kathiawar.

Age: Upper Burdigalian.

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TABLE 14

VARIATION IN EXTERNAL MEASUREMENTS

Lepidocyclina (Trybliolepidina) raoi Chatterji, n. sp.

Specimen no.	Diameter of test (mm.)	Thickness of test (mm.)	Diameter of central boss (mm.)
1	2.20	0.87	1.35
2	2.97	0.87	2.17
3	3.57	1.02	2.17
4	3.75	1.25	2.42
5	3.80	1.25	2.42

TABLE 15

MEASUREMENTS OF MEDIAN SECTIONS

Lepidocyclina (Trybliolepidina) raoi Chatterji, n. sp.

Dimensions	Specimen number			
	6	7	8	9
Diameter of test (in mm.)	3.80	3.75	3.57	2.20
Thickness of test (in mm.)	1.25	1.25	1.02	0.87
Ratio of D/T	2.0	2.9	3.4	2.5
Embryonic chambers:				
Diameter of protoconch	275.2μ	292.4μ	266.6μ	275.1μ
Diameter of deuteroconch	559.0μ	589.1μ	559.0μ	555.0μ
Ratio of D/P	2.0	2.0	2.0	2.0
Distance across both chambers	430.0μ	451.5μ	425.7μ	435.5μ
Thickness of partition wall	21.5μ	21.5μ	21.5μ	21.5μ
Thickness of outer wall	25.8μ	21.5μ	25.8μ	25.8μ
Equatorial chambers:				
Near center:				
Radial diameter	90.3μ	98.9μ	90.3μ	90.3μ
Tangential diameter	68.8μ	73.1μ	68.8μ	73.1μ
Near periphery:				
Radial diameter	75.4μ	75.4μ	81.7μ	75.4μ
Tangential diameter	60.2μ	60.2μ	68.8μ	60.2μ

TABLE 16

MEASUREMENTS OF VERTICAL SECTIONS

Lepidocyclina (Trybliolepidina) raoi Chatterji, n. sp.

Dimensions	Specimen number	
	10	11
Diameter of test (in mm).	2.97	2.77
Thickness of test (in mm.)	0.87	0.87
Ratio of D/T	3.4	3.1
Diameter of central boss (in mm.)	2.17	2.55
Width of flange (in mm.)	0.80	0.22
Thickness of flange	60.2μ	64.5μ
Embryonic chambers:		
Length	537.5μ	541.8μ
Height	176.3μ	184.8μ
Thickness of outer wall	30.1μ	25.8μ
Lateral chambers:		
Number of tiers on each side of equatorial layer	12	15
Length	111.8μ	107.5μ
Height	30.1μ	30.1μ
Thickness of floors and roofs	21.5μ	21.5μ
Surface diameter of pustules	124.7μ	107.5μ

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EXPLANATION OF PLATES

PLATE 1

1–6 *Lepidocyclina (Nephrolepidina) borneensis* (Provale)
1–2, external features of "Form A," from Loc. H (Bhogat), × 10; 3, external features of "Form B," from Loc. H (Bhogat), × 10; 4–5, median sections of "Form A," from Loc. H (Bhogat), × 30; 6, vertical section of "Form A," from Loc. Vf (Visawara), × 30.

7–10 *Lepidocyclina (Nephrolepidina) martini* (Schlumberger) var. *kamalae* Chatterji, n. var.
7–8, external features of "Form B," from Loc. H (Bhogat), × 10; 9–10, external features of "Form A," from Loc. H (Bhogat), × 10.

PLATE 2

1–4 *Lepidocyclina (Nephrolepidina) martini* (Schlumberger) var. *kamalae* Chatterji, n. var.
1–2, median sections of "Form A," from Loc. H (Bhogat), × 30 (2, holotype); 3, median section of "Form B", from Loc. H (Bhogat), × 30; 4, vertical section of "Form A," from Loc. H (Bhogat), × 30.

5–8 *Lepidocyclina (Nephrolepidina) morgani* (Lemoine and Douvillé)
5–6, external features of "Form A," from Loc. Vwl (Verawal), × 10; 7, median section of "Form A," from Loc. Vwl (Verawal), × 30; 8, vertical section of "Form A," from Loc. Vwl (Verawal), × 30.

9 *Lepidocyclina (Trybliolepidina) kathiawarensis* Chatterji, n. sp. External features of "Form B," from Loc. H (Bhogat), × 10.

PLATE 3

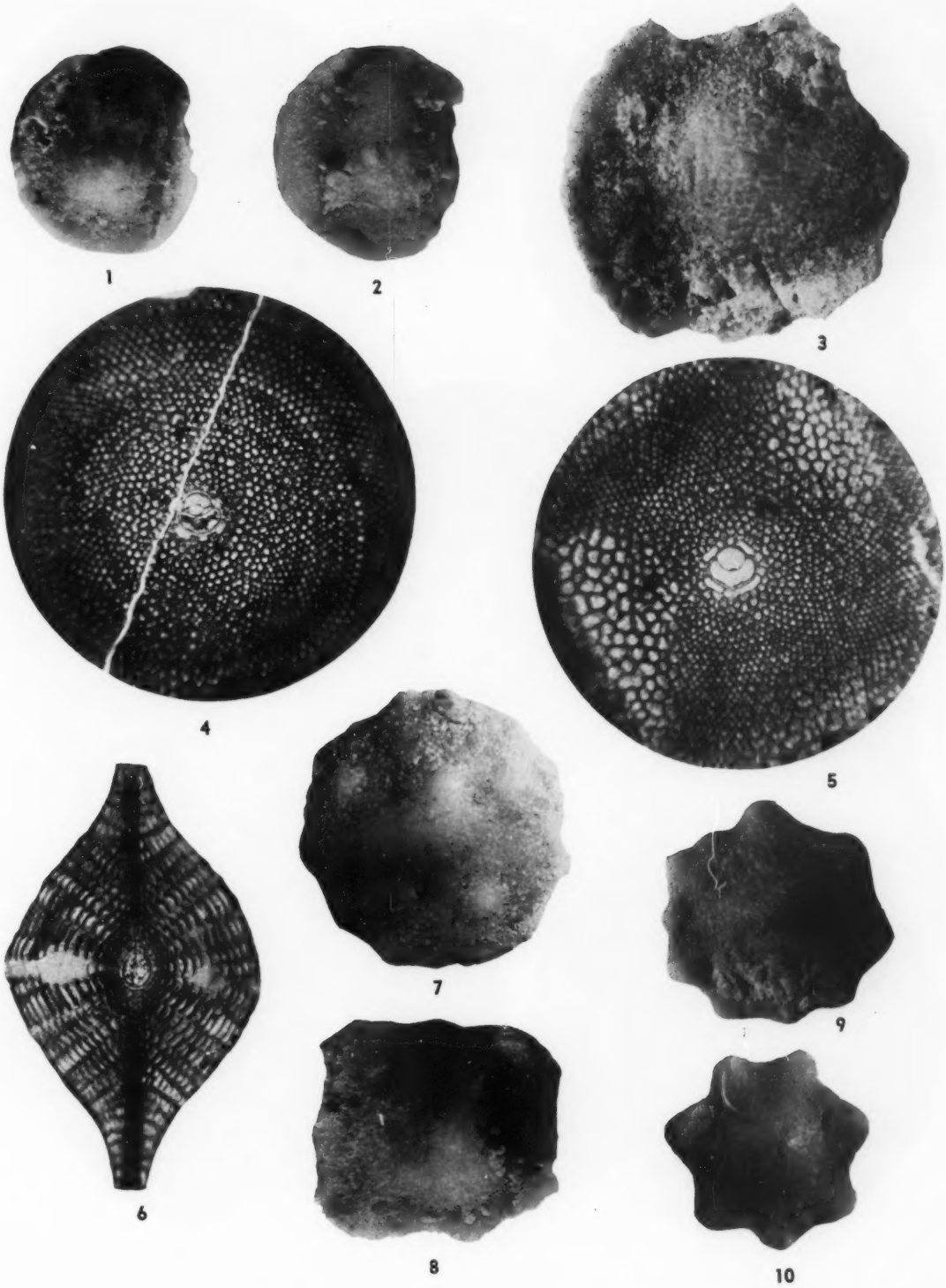
1–8 *Lepidocyclina (Trybliolepidina) kathiawarensis* Chatterji, n. sp.
1–3, external features of "Form A," from Loc. H (Bhogat), × 10; 4–7, median sections of "Form A," from Loc. H (Bhogat), × 30 (4, holotype); 8, vertical section of "Form A," from Loc. H (Bhogat), × 30.

PLATE 4

1–3 *Lepidocyclina (Trybliolepidina) kathiawarensis* Chatterji, n. sp.
1, median section of "Form B," from Loc. H (Bhogat), × 30; 2, vertical section of "Form B," from Loc. H (Bhogat), × 30, passing through the interstellate part of the test and showing single layer of equatorial chambers; 3, vertical section of "Form B," from Loc. H (Bhogat), × 30, passing through the stellate part of the test and showing the multiplication of the equatorial layer near the periphery of the test.

4–8 *Lepidocyclina (Trybliolepidina) raoi* Chatterji, n. sp.
4–5, external features of "Form A," from Loc. Vwl (Verawal), × 10; 6, vertical section of "Form A," from Loc. Vwl (Verawal), × 30; 7–8, median sections of "Form A," from Loc. Vwl (Verawal), × 30 (7, holotype).

9–10 *Lepidocyclina (Nephrolepidina) martini* (Schlumberger) var. *kamalae* Chatterji, n. var.
9, vertical section of "Form B," from Loc. H (Bhogat), × 30, passing through the stellate part of the test and showing the single layer of equatorial chambers throughout; 10, vertical section of "Form B," from Loc. H (Bhogat), × 30, passing through the interstellate part of the test and showing the single layer of equatorial chambers.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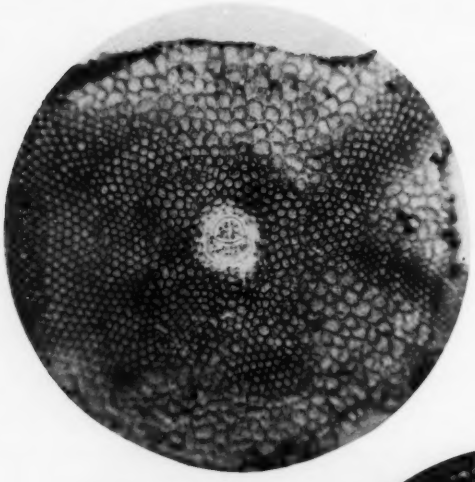

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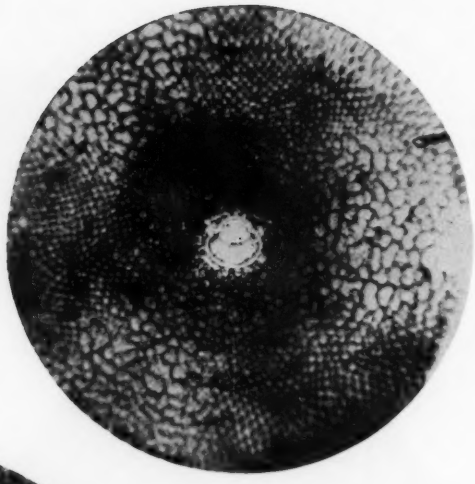

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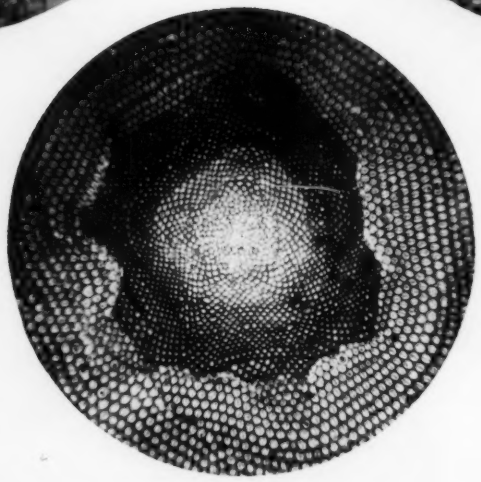

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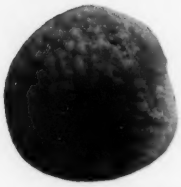

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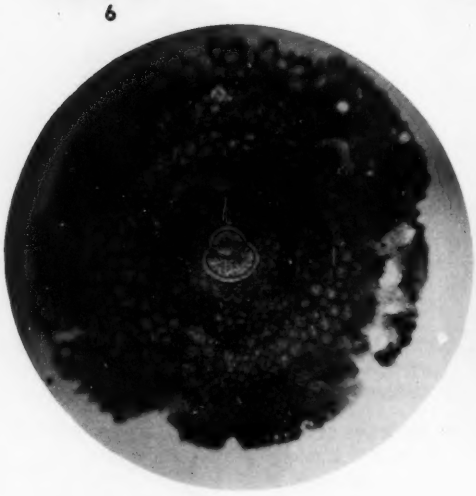

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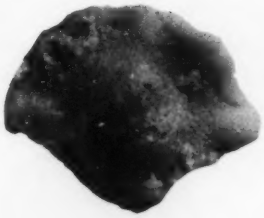

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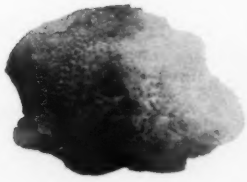

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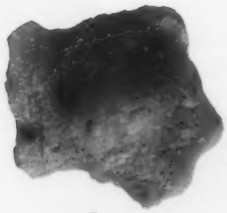

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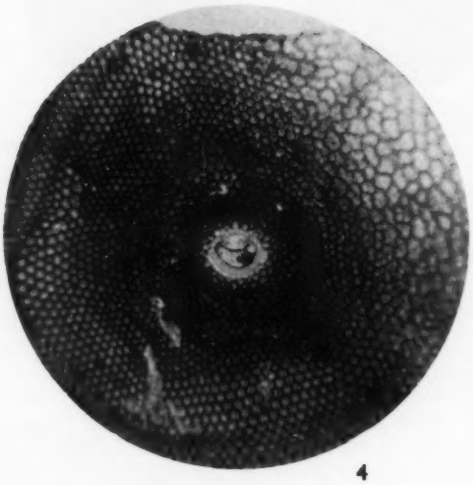

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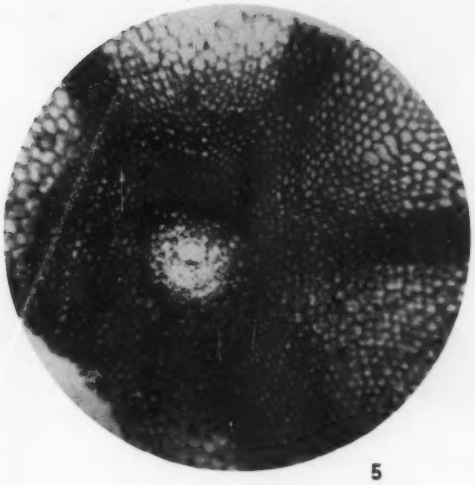

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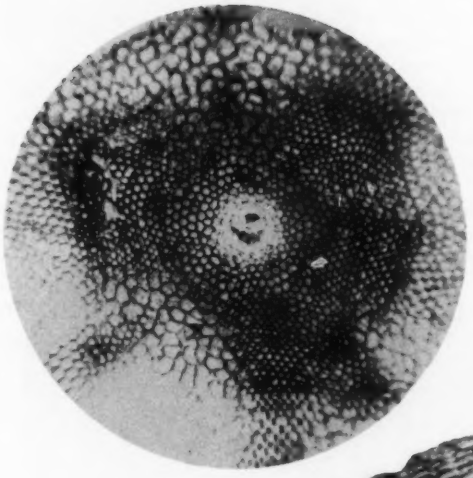

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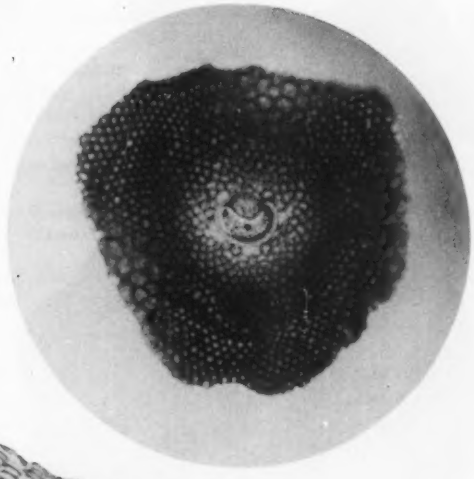

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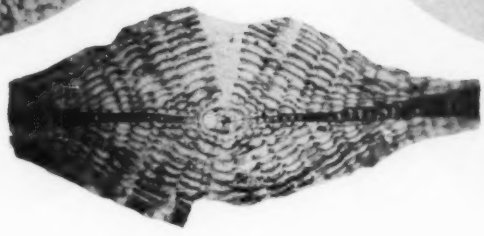

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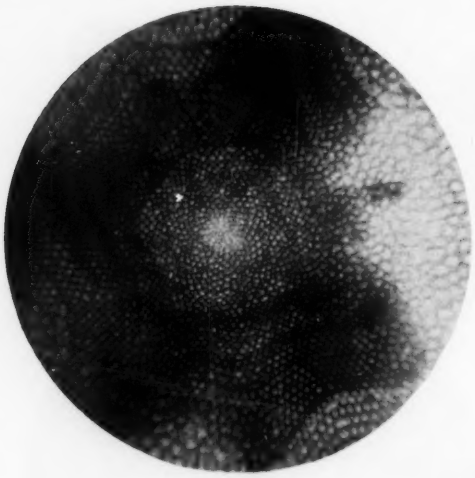

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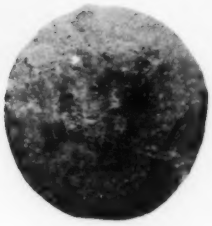

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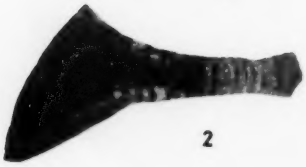

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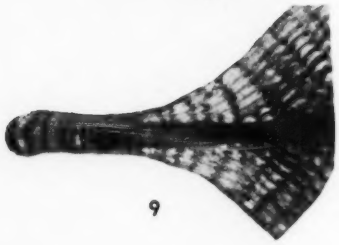

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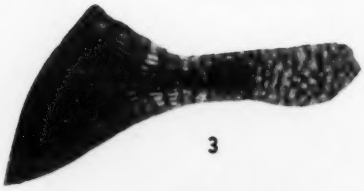

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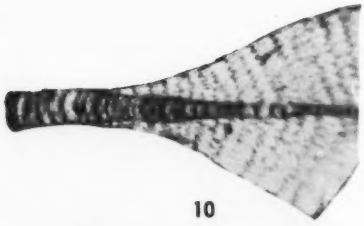

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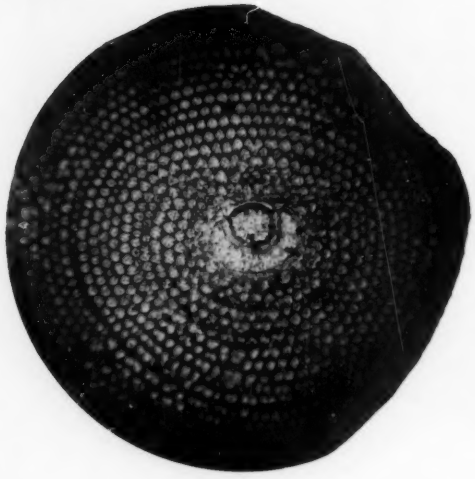

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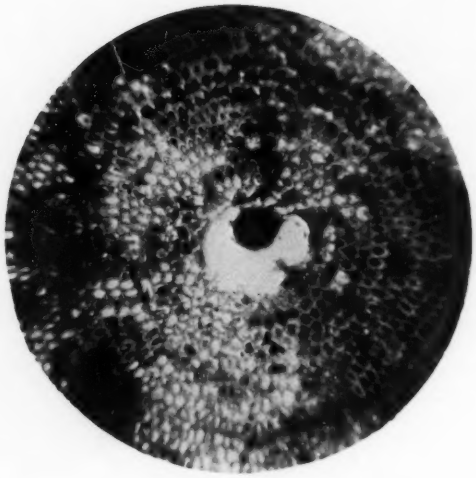

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ABSTRACT

Following a review of previous literature on Classopollis *Pflug, 1953 and a discussion of its nomenclature, type species, and diagnosis, this pollen genus is here emended on the basis of numerous specimens recovered from Permian to Upper Cretaceous rocks in Canada. The type species,* Classopollis classoides *Pflug, is also emended, and three new species are described. The stratigraphic occurrence, possible depositional environment, and possible affinities of the genus are discussed.*

The pollen genus Classopollis Pflug, 1953

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INTRODUCTION

Pollen grains referable to the genus *Classopollis* Pflug are found in strata ranging in age from Permian to Eocene. Some Jurassic and Lower Cretaceous horizons in many parts of the world have yielded many thousands of well-preserved grains referable to this genus. Despite this abundance of well-preserved material, most published descriptions of species assignable to the genus, including the original generic description and subsequent emendations, are both inadequate and inaccurate. The position regarding nomenclature is no better, a combination of misinterpretation and of failure by some authors to check the synonymy sufficiently closely having resulted in a nomenclatural situation that is little short of chaotic. In the following paragraphs, the authors give some account of previous literature referring to this genus and an interpretation of it based on specimens isolated from Canadian strata, together with descriptions of a few Canadian species.

ACKNOWLEDGMENTS

The authors wish to thank Dr. H. D. Pflug, of Giessen, for correspondence regarding the genus *Classopollis* and for the loan of comparative material, and Dr. R. Potonié, of Krefeld, for the discussion of some problems relating to the genus. They also express thanks to the editors of *Palaeontographica*, and in particular Professor H. Weyland, for permission to reproduce the original figure of the holotype of *Pollenites torosus* Reissinger (pl. 1, fig. 13, of the present paper) and two figures of specimens assigned by Thiergart to his species *Bennettiteae-Pollenites reclusus*, and to Imperial Oil Limited for permission to publish this paper.

PREVIOUS LITERATURE

1933 – Pollen of *Cheirolepsis muensteri* Schenk. – HOERHAMMER, 1933, p. 134, pl. 4, fig. 27Aaa and Aab.

Hoerhammer discussed and illustrated pollen grains as those of *Cheirolepis muensteri* Schenk which appear identical to some of the dispersed grains assigned to *Classopollis*.

1949 – *Bennettiteae-Pollenites reclusus* Thiergart. – THIERGART, 1949, p. 11, pl. 2, figs. 14–16; pl. 3 fig. 6.

Pollen grains referred to this species of Thiergart have been cited as identical with *Classopollis classoides* Pflug by some authors. The specific description is, however, inadequate, and the plates are very poor, making positive comparison impossible. Pflug, who has examined Thiergart's type material, is of the opinion that the two species are quite distinct (personal communication).

1949 – Pollen grains of *(?) Brachyphyllum scottii* Kendall. – KENDALL, 1949, p. 307, text-fig. 1, J and K.

These pollen grains were described as 30–40μ in diameter, each bearing two wide bands of thickening sharply demarcated from the thinner polar and equatoral regions. The illustrations show a single grain and a tetrad which clearly belong to Pflug's genus *Classopollis*. The diagrams show a circular distal pore very clearly, a feature not recognized by many subsequent authors. These grains were found in association with megafloral remains of *Brachyphyllum scottii* Kendall, some being still attached to a male cone axis which probably belonged to that species.

1950 – *Pollenites torosus* Reissinger. – REISSINGER, 1950, p. 115, pl. 14, fig. 20.
Pollen of *Cheirolepis muensteri* Schenk. – REISSINGER, 1950, p. 114, pl. 14, figs. 10–14.
Conifer pollen. – REISSINGER, 1950, pl. 14, figs. 15–16; pl. 18, fig. 32a–b.
Conifer pollen. – REISSINGER, 1950, pl. 14, figs. 21–28.

In this paper, Reissinger described a series of grains which can be referred to Pflug's genus *Classopollis*, but only one specific name was proposed, *Pollenites torosus*. He compared these pollen grains with grains from male cones assigned to *Cheirolepis muensteri* Schenk and concluded that there is a definite natural relationship between the two types.

1952 – Pollen of *Pagiophyllum connivens* Kendall. – KENDALL, 1952, pp. 583–594.

Kendall described pollen grains from an araucarian male cone attributed to *P. connivens*. The grains were circular to oval, scabrate, with a thickened equatorial region. These grains have been compared with *Classopollis classoides* Pflug by some authors.

1953 – *Aporina striatella* Bolkhovitina. – BOLKHOVITINA, 1953, p. 101, pl. 16, fig. 36.

This species, although larger than any described by Pflug, appears to be referable to the genus *Classopollis*.

1953 – *Classopollis classoides* Pflug. – PFLUG, 1953, p. 91, pl. 16, figs. 20–25, 29–37.
Classopollis declassis Pflug. – PFLUG, 1953, p. 92, pl. 16, figs. 16–19.
Tetrads of *Classopollis* Pflug. – PFLUG, 1953, pl. 16, figs. 29–30.
Circumpollis pharisaeus Pflug. – PFLUG, 1953, p. 92, pl. 17, figs. 28–30.
Circumpollis philosophus Pflug. – PFLUG, 1953, p. 92, pl. 17, figs. 31–36.
Canalopollis maturus Pflug. – PFLUG, 1953, p. 93, pl. 17, figs. 48–60.

In this paper Pflug erected the genus *Classopollis*. Although the authors cannot accept his interpretation of the structure of this genus, the illustrations of the holotype (pl. 16. figs. 29–31) appear to them to be perfectly clear; these figures, together with the supplementary ones (figs. 20–25 and 32–37), leave no doubt as to the forms of pollen which should be assigned to the genus.

In addition to *Classopollis*, Pflug erected two other genera, *Circumpollis* and *Canalopollis*, which comprise very similar grains. Many workers dispute the validity of these two genera, and there appears to the authors to be little merit in separating these genera from the genus *Classopollis*. The action of Couper (1955 and 1958) in assigning all the forms that Pflug had described under the three genera to the one species *Classopollis torosus* appears, however, to be the other extreme.

1954 – *Tetradopollenites reclusus* (Thierg.). – SITTLER, 1954, pp. 338–341.

The generic name *Tetradopollenites* was applied by Sittler to species similar to Thiergart's *Bennettiteae-Pollenites reclusus* and habitually occurring in tetrads; it was presumably intended to include species falling in the genus *Classopollis*. As far as the authors can determine, this generic name was not validly published.

1954 – *Brachyphyllum* Brongn. – ZAUER AND MCHEDLISHVILI, 1954, pp. 7–9.

The stratigraphic value of pollen grains resembling those obtained by Kendall in 1949 is discussed. The grains pictured here appear identical to species assigned by Pflug to *Classopollis*.

1954 – Cheirolepidaceae Groups I–IV. – ROGALSKA, 1954, pl. 11. figs. 1–10.

Many of the specimens illustrated and described by Rogalska can be placed in the genus *Classopollis*. The validity of her four groups appears to be doubtful.

1955 – Tetrads of operculate grains. – KUYL, MULLER AND WATERBOLK, 1955, pl. 6, figs. 9–11.

Tetrads of grains which are certainly referable to the genus *Classopollis*, probably the species *C. classoides* Pflug, were illustrated.

1955 – *Trachytriletes* Type 3(?). – SAH, 1955, p. 63, pl. 1, fig. 6.
Liratoaletes Type 1. – SAH, 1955, p. 65, pl. 1, fig. 11–11a.
Liratoaletes Type 2. – SAH, 1955, p. 65, pl. 1, fig. 16.
Striatoaletes Type 1. – SAH, 1955, p. 64, pl. 1, fig. 18.
Trachyaletes Type 1. – SAH, 1955, p. 64, pl. 1, fig. 25.

The forms assigned to these groups appear to be referable to the genus *Classopollis*. Poor descriptions and illustrations make specific comparison impossible. It appears from the illustrations that Sah misinterpreted different orientations of the same species as different forms. His names *Liratoaletes*, *Striatoaletes*, and *Trachyaletes* are not valid since they are not properly described as new genera, and no type species are proposed.

1955 – *Classopollis*, *Circumpollis*, and *Canalopollis* types of pollen, – COUPER, 1955, pp. 471–474, pl. 20, fig. 8; pl. 21. figs. 1–10.
Pollen from an araucarian male cone attributed to *Pagiophyllum connivens* Kendall. – COUPER, 1955, pp. 472–474, pl. 21, figs. 11–12.

Couper's opinions regarding these forms will be discussed more fully in a later paragraph.

1955 – *Classopollis* Pflug. – KRUTZSCH, 1955, pl. 4, fig. 42.
cf. *Classopollis* Pflug – KRUTZSCH, 1955, pl. 4, figs. 51–52.
Circumpollis Pflug. – KRUTZSCH, 1955, pl. 4, figs. 45–47.
Altmark W-20 form. – KRUTZSCH, 1955, pl. 4, fig. 43.
Altmark W-21 form. – KRUTZSCH, 1955, pl. 4, figs. 48–49.
Altmark W-22 form. – KRUTZSCH, 1955, pl. 4, figs. 55–56.
Altmark W-23 form. – KRUTZSCH, 1955, pl. 4, fig. 57.
Altmark W-24 form. – KRUTZSCH, 1955, pl. 4, figs. 58–60.
Altmark W-25 form. – KRUTZSCH, 1955, pl. 4, fig, 61.
Altmark W-26 form. – KRUTZSCH, 1955, pl. 4, figs. 62–63.
Altmark W-27 form. – KRUTZSCH, 1955, pl. 4, fig. 64.
cf. Form Reissinger (1950 pl. 14, figs. 21, 27–28). – KRUTZSCH, 1955, pl. 4, fig. 44.
cf. Form Reissinger (1950, pl. 14, figs. 15–16). – KRUTZSCH, 1955, pl. 4, fig. 50.
cf. Form Reissinger (1950, pl. 14, fig. 20). – KRUTZSCH, 1955, pl. 4, figs. 53–54.

1957 – *Classopollis* cf. *C. torosus* (Reissinger). – BALME, 1957, pl. 11, figs. 114–119.
Classopollis sp. – BALME, 1957, pl. 11, figs. 120–122.

In this paper, Balme assigned Reissinger's species *Pollenites torosus* to Pflug's genus *Classopollis*. Although the authors agree with such an assignment, it appears to them that Balme's figured specimens appear closer to Pflug's species *C. classoides* than to Reissinger's *P. torosus*.

1958 – *Classopollis torosus* (Reissinger). – COUPER, 1958, pp. 156–157, pl. 28, figs. 2–7.

In this work, Couper amended Pflug's diagnosis of *Classopollis* and proposed Reissinger's type of the species *torosus* as the genotype on grounds of synonymy. He also repeated the arguments brought forward in 1955 for assigning all of Pflug's species of *Classopollis*, *Circumpollis*, and *Canalopollis* to the one species *Classopollis torosus* and for regarding them as identical with the pollen of *Pagiophyllum connivens* Kendall.

1958 – *Tetradopollenites reclusus* (Thierg.) Sittler. – LANTZ, 1958, p. 928, pl. 7, figs. 71–72.

Lantz refered spherical, operculate, striate grains with a vestigial trilete mark to this species, which she regarded as synonymous with *Classopollis torosus* (Reissinger) Couper (1958). The dimensions and structure of the figured grains appear, however, to be identical with Pflug's species *Classopollis classoides*.

1959 – *Pterocarya poropollenites* Rouse. – ROUSE, 1959, pl. 1, figs. 21–22.

The grains thus described by Rouse are, in the authors' opinion, rather corroded *Classopollis* grains. The authors have frequently observed such grains in samples from the Western Canadian foothills and mountains, which have suffered some alteration (metamorphism). Both of Rouse's figured specimens appear to be equatorially striate, and the specimen in figure 21 shows what appears to be a vestigial trilete. The dimensions of Rouse's specimens fall well within the range of *Classopollis classoides* Pflug.

1959 – KLAUS, 1959, p. 161.

A diagram illustrates a pollen tetrad which appears to belong to the genus *Classopollis*, from the Karnian (Upper Triassic) of the European Alps.

VALIDITY OF THE GENERIC NAME CLASSOPOLLIS PFLUG, 1953

Despite a host of names applied to the type of pollen under discussion, only two are possibly applicable:

CLASSOPOLLIS PFLUG, 1953

Pflug's description and photographs of the type species for this genus are quite clear; the generic name is thus perfectly valid under the rules of nomenclature, and has priority over the following name.

TETRADOPOLLENITES SITTLER, 1954

The assignment of the generic name *Tetradopollenites* to Thiergart's species *reclusus* might be argued as valid on the grounds that Thiergart's binomial generic name *Bennettiteae-Pollenites* is invalid. The assignment of Reissinger's *Pollenites torosus* and Pflug's *Classopollis classoides* to this species by Lantz and by Couper on grounds of synonymy is unwarranted, however, since such synonymy cannot be proven. It is doubtful if the generic name *Tetradopollenites* was validly published. The only reference that the authors can find to the original assignment of the name is a report of a lecture by Sittler in 1954, in which the name was mentioned. This would invalidate the name under Article 33, Provisions 2 and 3, of the International Code of Botanical Nomenclature.

All subsequently published generic names for the forms of pollen under discussion are invalid on grounds of priority of publication. Botanical organ-genera are not included in this discussion, since the authors consider that the mixing of natural and morphological terminology can only lead to confusion.

THE TYPE SPECIES OF CLASSOPOLLIS

Pflug (1953) proposed the species *Classopollis classoides* as the type for his genus *Classopollis*. The genotype is illustrated in plate 16, figures 29–31, of his 1953 paper, and it is from these figures only, together with the generic diagnosis and specific description, that the validity of the type species must be judged. If a previously validly named species can be shown to be identical with Pflug's genotype, it will automatically replace Pflug's species as the genotype of *Classopollis*, provided its holotype is in existance. Thus, if Thiergart's species *Bennettiteae-Pollenites reclusus* (1949) and Reissinger's *Pollenites torosus* (1950) are identical with *Classopollis classoides* Pflug (1953), Thiergart's *reclusus* will take precedence and become the genotype of Pflug's genus *Classopollis*.

Couper's rejection of Thiergart's species *reclusus* in favor of Reissinger's *torosus* on the grounds of invalidity of the binomial generic name for Thiergart's species is inadmissible under Article 70(3) of the International Code. In actual fact, however, it cannot be shown beyond reasonable doubt that either Thiergart's or Reissinger's species is identical with the genotype *Classopollis classoides* Pflug. In spite of the poor preservation of Thiergart's type, the authors are of the opinion that the two species are different. Pflug, who has examined Thiergart's type material, holds the same opinion.

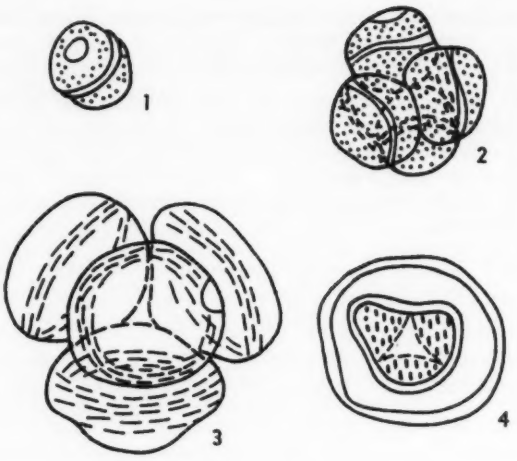
The type specimen of Reissinger's *Pollenites torosus* is shown in plate 14, figure 20, of his 1950 paper. The holotype itself is no longer in existence. Figures 15 and 16 on the same plate (particular figure 16) appear to be close to, if not identical with, the holotype of *Classopollis classoides* Pflug, and Pflug himself is in agreement with such a comparison. Reissinger, in the description of this plate and in the text (top of page 115), made it

perfectly clear that he regarded *Pollenites torosus* as a quite distinct and different species from the grains illustrated in figures 15 and 16, and comparison of the figures and descriptions of the two forms leads the authors to agree with this conclusion. Thus, it would appear that *Pollenites torosus* Reissinger and *Classopollis classoides* Pflug are not identical. *Classopollis classoides* Pflug holds priority over all subsequently described forms assignable to the genus and therefore remains the valid genotype.

GENERIC DIAGNOSIS

Pflug's (1953) generic diagnosis of *Classopollis* was: "tricolporate, rarely tetracolporate. Rimula well developed, germinales gaping. Poles never quite identical in appearance." In the text (pp. 73–74) he illustrated the position of what he termed the "rimula", or main colpus. The exine structure of many specimens also appears to support the theory that *Classopollis* possesses characters in common with both gymnosperms and angiosperms. Our figure 5 on plate 1 illustrates a grain from the Neocomian of Alberta which belongs to the genus *Classopollis* and has the appearance of a tricolpate grain with a two-layered tectate exine. Oblique squashing caused this misleading appearance.

Couper (1955 and again in 1958) criticized Pflug's interpretation, and compared *Classopollis* pollen with that from *Pagiophyllum connivens* Kendall, concluding that *Classopollis* pollen was derived from that or a related plant. In his 1958 paper he emended Pflug's diagnosis to: "Pollen grains circular to oval in polar view; equatorial region with distinct intexinal thickening; exine of polar regions comparatively thin, scabrate; proximal pole usually showing a vague tetrad marking, taking the form of a weak area in the exine." He designated Reissinger's *Pollenites torosus* as genotype, and noted that the genus is intended for the reception of dispersed pollen grains of the type met with in *Pagiophyllum connivens*. The authors, although agreeing that Pflug's original diagnosis is inaccurate, feel that Couper's emendation is unsatisfactory. In demonstrating the affinity between *Classopollis* and *Pagiophyllum connivens*, he stated: "Unfortunately, the pollen [i.e., of a *Pagiophyllum* male cone] preparation is rather deeply stained, undermacerated ... and not clearly displayed." He therefore referred to his own "detailed description of *Classopollis torosus* (Reiss.) Couper,...based on hundreds...of dispersed grains." Then, in turn, in this description he stated that the wide "range of variation of the grains of *Pagiophyllum connivens*" warrants lumping all of Pflug's species and genera into this one species. The implied relations between these grains and the pollen of *Pagiophyllum connivens* is not proven, and thus the suggestion that the genus *Classopollis* should receive grains of the type met with in *Pagiophyllum connivens* is unwarranted. In any case, even in the most excellent preparations of associated microspores, we may expect the range of variation to be wider than in dispersed grains because of the immaturity of some of the grains.



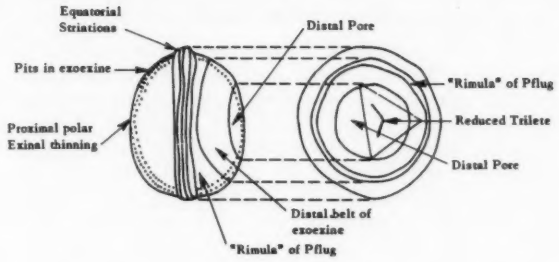
TEXT-FIGURES 1–4

1–2 (after Kendall, 1949), single grain and tetrad from male cone axis attributed to *Brachyphyllum scottii* Kendall; 3–4 (after Zauer and Mchedlishvili, 1954), pollen grains of "*Brachyphyllum*": 3, tetrad; 4, distal polar view of single grain showing "laceration" and vestigial trilete.

Balme (1957), although not proposing any formal emendation of Pflug's generic diagnosis, noted Pflug's misinterpretation of the structure of the grain and described two species of *Classopollis* as having the following characters in common: "Amb round or oval, flattened acorn-shaped in lateral view. Vestigial trilete markings often present in the form of a triangular or triradiate scar on the proximal face. Germination apparently by means of distal operculum. Exine thickened in a narrow equatorial zone which appears as an equatorial rim in polar view." Particularly significant in this description is the mention of a distal operculum. No such operculum was mentioned in Couper's diagnosis.

Two other contributions, although not specifically referring to the genus *Classopollis*, describe grains that belong to that genus and are important for purposes of interpretation. Kendall (1949) illustrated a grain and a tetrad of pollen grains recovered from a male cone axis, probably referable to the species *Brachyphyllum scottii*. She described the grains as "round, 30–40μ in diameter, and thickly cutinised. Each bears two wide bands of thickening, sharply demarcated from the thinner polar and equatorial regions....The exine is not granular." The illustrations (text-fig. 1J and K) show grains that unquestionably belong to the genus *Classopollis*, each possessing a distal pore, a character not noted by many subsequent authors.

Zauer and Mchedlishvili (1954), following Kendall's (1949) interpretation of the affiliation, described pollen of the *Classopollis* type under the generic name *Brachyphyllum*, as follows: "The grains of this pollen usually



TEXT-FIGURE 5

occur in tetrads, seldom only in single grains. The grain is round-ellipsoidal. No pores or furrows. The capsule is multilaminated, thicker at the proximal side of the grain and thinner at the distal side. The grain shows an equatorial swelling with parallel striae, which are interrupted at one point only. Some grains have traces of a tetrad scar preserved. The distal side of the grain is sometimes lacerated. The color of the grain varies between light and dark brown." Although distal "laceration" of some grains was noticed, there was no mention of a distal pore, although this feature was shown in Kendall's illustrations. The figures accompanying their description also fail to show such a feature.

In the course of studying the microflora of Western Canada, many hundreds of well-preserved pollen grains assignable to the genus *Classopollis* were recovered from samples ranging in age from Permian to Upper Cretaceous, a majority of the specimens being obtained from samples of Middle and Upper Jurassic age. Many of the specimens resemble *Classopollis classoides* Pflug 1953. This identification was confirmed by Pflug, who examined some of the Canadian material and loaned the authors a slide containing some of his own specimens. With the aid of this well-preserved material, the authors propose to emend the generic diagnosis of *Classopollis* and to describe some of the Canadian species assignable to that genus.

SYSTEMATICS

Genus Classopollis Pflug, 1953, emended, Pocock and Jansonius

Diagnosis: Pollen grains; distally monoporate; ovoid, spherical, or flatly acorn-shaped; exine two-layered; exoexine absent or much reduced over a circular area surrounding the distal pole, and absent or reduced over a triangular area with its center at the proximal pole; intexine frequently bearing a reduced trilete scar, which has no germinal function, at the proximal pole; exine always ornamented by striations in a band or girdle surrounding the equator and interrupted (if at all) at only one point; the band usually, but not always, marking a zone of exinal thickening.

Type species: Classopollis classoides Pflug, 1953.

Classopollis classoides Pflug, emended, Pocock and Jansonius
Plate 1, figures 1–9

"Conifer pollen," Reissinger, 1950, p. 114, pl. 14, figs. 15–16.
Classopollis classoides Pflug, 1953, p. 91, pl. 16, figs. 29–31.

Description: Spherical, ovoid, or flatly acorn-shaped; circular in equatorial section; monoporate, with a circular distal pore 12–15μ in diameter; exine two-layered; intexine thin (about 1μ thick), laevigate, continuous over whole area of spore, occasionally showing a small trilete mark at the proximal pole, which does not function as a germinal aperture; rays of trilete, where present, not more than 3μ long; exoexine 1–2μ in thickness, divisible into two distinct zones; a wider zone enveloping the proximal hemisphere and a smaller zone forming a belt of exoexine, averaging 5μ in width, surrounding the exposed intexine of the distal pole; the distal belt is separated from the exoexine of the proximal hemisphere by a narrow band of exinal thinning slightly distal to the equator, over which the exoexine is absent or reduced (this band forms the "rimula" of Pflug); the exoexine of the proximal hemisphere is absent over a triangular area surrounding the proximal pole and thickens toward and over the equator; four or more annular bands of exoexinal thickening, which may or may not be quite pronounced, form a belt averaging 9μ in width surrounding the equator; exoexinal ornament appears to consist of small pits, distributed radially to the surface of the grain and frequently fusing at the surface to form continuous bands of ornamentation around the equator, and of a granulose or in some instances microreticulate pattern over the rest of the exoexine. (It is extremely easy to confuse this type of ornamentation with a tectate exine, which is, in fact, exactly the reverse structure, being made up of rods and not pits.)

Color of spore: Light yellow to deep yellowish brown.

Size range: Polar diameter 18 (23) 24μ; equatorial diameter 21 (29) 33μ.

Remarks: This species is very distinctive and easy to recognize. Plate 1, figure 1, shows a photograph of one of Pflug's specimens from the Lias of Siegelsum well no. 2, and figure 2 shows an enlargement of one grain of the tetrad. Figure 3 shows a tetrad from the Middle Jurassic of Saskatchewan, and figure 4 an enlarged grain assigned to the same species, showing quite clearly the distal pore and distal exoexinal belt, which occasionally pulls away from the equatorial belt in two diametrically opposite places. Both Pflug and the authors of this paper would assign all four specimens to the species just described. Figure 8 and 9 show a tetrad and a single grain from that tetrad, also assignable to *C. classoides* Pflug. These specimens are exceedingly well preserved and show the details of the ornament, the two-layered exine, and the nature of the distal pore very well. Figures 6 and 7 are a diagram and a photograph of the structure of a corroded grain

of *Classopollis* cf. *classoides*, showing the relationship between the proximal pole with reduced trilete mark and the distal pore.

Classopollis belloyensis Pocock and Jansonius, new species

Plate 1, figures 10–12

Description: Pollen grains; more or less circular in polar section; exine two-layered; intexine thin, scabrate, brownish yellow in color, constituting a globular central body; exoexine much thicker, averaging 2μ but increasing to 6μ in the equatorial region; pale yellow to colorless, hyaline, slightly roughened, enveloping the central body except at the distal and possibly at the proximal pole; at the distal pole the exoexine is absent over a circular area 12μ in diameter, forming a distal pore. Exoexine thickened in the equatorial area, forming a broad girdle, 12μ wide, which carries ornamentation consisting of eight to ten parallel equatorial ridges and grooves, possibly interrupted at one point; this ornamentation does not show up very clearly in outline, suggesting the possibility that it may be internal and caniculate in character. The symmetry is probably radial, but possibly bilateral, if the equatorial girdle has its greatest expansion in two opposite areas on the equator (cf. *Vittatina*). Pyrite crystals within the grain prevent observation of any proximal polar structures.

Size: Equatorial diameter about 38μ; polar diameter about 30μ.

Holotype: Imperial Belloy 12–14 (12–14–78–1W6M), at 4227 feet; locality approximately 180 miles northwest of Edmonton, Alberta, Canada. Slide No. Imp. H–385–2 (116.0'–27.2).

Stratigraphic position: Lower (carbonate) member, type section, Belloy formation. This falls about in the middle of the Upper Permian (Guadeloupean?).

Discussion: In appearance and stratigraphic position, this species agrees with what one would expect of the forerunner of the several Mesozoic *Classopollis* species. The holotype is well preserved, and several other specimens were observed in the same sample, which otherwise carries a dominantly marine assemblage. Jansonius recorded the same species from samples of shale and siltstone from the Hilton Plant Beds of Westmorland, England, which are of about the same age. Plate 1, figure 10, shows a photograph of the holotype. Figure 11 is an enlarged view of the same specimen, showing the exoexinal ornament, and figure 12 is a similar photograph, showing details of the scabrate endexine of the distal pore.

Classopollis minor Pocock and Jansonius, new species

Plate 1, figures 21–25

"Conifer pollen," REISSINGER, 1950, p. 114, pl. 14, figs. 21–28; pl. 18, fig. 33a–e.

cf. "Siegelsum N. Typus," PFLUG, 1953, pl. 17, figs. 38–40.

"Cheirolepidaceae Group II," ROGALSKA, 1954, p. 23, pl. 11, figs. 4–6.

Description: Pollen grains; oval to circular in polar section, circular in equatorial section; exine two-layered; intexine thin, laevigate; exoexine thicker (1–3μ), divisible into two zones; one zone envelops the proximal hemisphere but for a triangular aperture at the proximal pole, 5–7μ in diameter, through which the intexine is exposed; the other exoexinal zone envelops the distal hemisphere and carries a circular aperture about 4μ in diameter at the distal pole, where the intexine is exposed, forming a distal pore; this zone meets the exoexine of the proximal hemisphere approximately at the equator and is separated from it by a very narrow band where the exoexine is absent or very much thinned; this band of thinning is relatively less well developed than in *Classopollis classoides* Pflug; ornament of exoexine internally caniculate; exoexine of proximal hemisphere thickened in the equatorial area, forming a girdle about 6μ wide, ornamented by about ten parallel canals within the exine, which show a break at one point; a second series of similar canals is developed parallel to each side of the triangular proximal exoexinal aperture; these canals are truncated by the equatorial girdle; distal exoexine ornamented by a series of radially disposed pits, which are frequently united at the surface, giving the appearance of microreticulate ornamentation; grains usually deep yellow brown in color.

Size range: Equatorial diameter 21 (25) 27μ (holotype 25μ); polar diameter 21 (22) 24μ (holotype 22μ).

Holotype: Tidewater Southey 4–29–22–18W2M, at 2276–77 feet (south-eastern Saskatchewan); Gravelbourg formation (Bajocian). Slide No. 2119–1 (35.6–119.3).

Stratigraphic range: Lower Jurassic to Eocene; most abundant in Canada in the Middle and Upper Jurassic, where it appears in great abundance at some horizons. There appears to be little relationship between the abundance of this species and that of other species of the same genus at any one horizon, which suggests that these grains were derived from a natural species of plant distinct from those producing other species of *Classopollis* pollen.

Remarks: These grains are smaller than those of other described species of *Classopollis*, and the striation around the proximal aperture makes them very distinctive. The grains are usually seen in polar view, and tetrads are rare. Plate 1, figures 23–24, the holotype, shows the grain in equatorial view; figures 21 and 22 show distal and proximal polar views, respectively; figure 25 is an oil-immersion photograph of the proximal view of a grain, showing the striation parallel to the sides of the aperture and the band of thinning parallel to the equator marking the line of division between the proximal and distal exoexine (the "rimula" of Pflug).

Classopollis pflugii Pocock and Jansonius, **new species**
Plate 1, figures 16–20

"Possibly Taxodeacean pollen" REISSINGER, 1950, pl. 14, figs. 18–19

Description: Pollen grains; oval in polar section, circular in equatorial section; exine two-layered; intexine thin, laevigate, translucent; exoexine about 1.5μ thick, transparent, loosely enveloping the intexine, which forms a more or less spherical central body; exoexine divisible into two zones, one enveloping the proximal hemisphere and carrying a faint trilete mark at the proximal pole, the other enveloping the distal hemisphere and thinning over a circular area around the distal pole, although no distinct distal pore appears to be developed; this thinned area is frequently torn or distorted, indicating that it is a definite area of exinal weakness; it probably functioned as a germinal area. The two exoexinal zones are separated by a narrow unornamented band of exinal thinning; ornament of exoexine internally caniculate; exoexine of proximal hemisphere thickened in the equatorial region, forming a girdle about 6μ wide ornamented by about seven canals within the exoexine, which show a break at one point; the remainder of the exoexine, with the exception of the laevigate "rimula," is ornamented by a series of small pits distributed radially to the surface of the grain; it is characteristic of this species that the exoexine is only very loosely attached to the intexine, and this frequently results in the intexinal central body becoming detached from the exoexine; grains usually light yellow to yellowish brown in color.

Size range: Central body 21.0 (21.9) 22.8μ × 15.0 (16.5) 18.0μ (holotype 22.8μ × 18.0μ); whole grain 26.4 (28.3) 33.0μ × 21.0 (23.2) 27.0μ (holotype 26.4μ × 21.6μ).

Holotype: Blackfoot Devonian Test Syndicate No. 1, 12–15–50–2W4M, at 2014–26 feet. Slide No. 3510 (2014–26)–1(41.4–126.9).

Stratigraphic range: This species has been recognized only from the Lower Cretaceous of Western Canada, where its geographic distribution is somewhat restricted. Similar forms have, however, been seen in Upper Jurassic sediments of Western Canada, although these are not specifically identical. Two grains illustrated by Reissinger (see the synonymy) from the Upper Jurassic of Europe appear to be similar, if not identical, to this species. Some grains assignable to this species have been squashed in a direction parallel to the polar axis, resulting in the exoexine becoming folded around the equator to form a thick girdle. Such grains resemble fairly closely Reissinger's figure of his species *Pollenites torosus* (1950, pl. 14, fig. 20) (see pl. 1, fig. 13, of the present paper), although the poor quality of Reissinger's figure and the lack of an adequate specific description prevent any positive comparison of the Canadian specimens with Reissinger's species. If *C. pflugii* is, in fact, identical with any of Reissinger's specimens, its range is immediately extended, becoming Upper Jurassic to Cretaceous.

Remarks: Figure 20 is a photograph of the holotype, and figure 19 an oil-immersion photograph of the same specimen. Figure 17 shows an isolated torn exoexine of a grain of the same species, the central body having been lost. Figure 16 shows a folded tetrad which should be compared with figure 13, the holotype of *Pollenites torosus* Reissinger. Figure 18 shows a distal polar view of a grain assigned to this species.

MORPHOLOGICAL CHARACTER OF CLASSOPOLLIS

The descriptions of the preceding four species are not intended as a comprehensive account of species assignable to the genus, but merely to illustrate typical morphological characters. The principal features of the genus which appear to vary significantly from species to species and permit reliable specific differentiation to be carried out, appear to the authors to be:

1) The thickness of the exoexine and the tightness or looseness of its attachment to the central intexine.

2) The degree of differentiation of the exoexine into proximal and distal zones.

3) The degree of thickening of the equatorial girdle and the nature and distribution of its striate ornamentations.

4) The nature of the ornamentation of the distal and proximal exoexine. The extent of development of such ornamentation is, as pointed out by several previous authors, somewhat variable, dependent upon the extent of corrosion of the grain, but the basic pattern of ornamentation remains constant for any species so long as the exoexinal layer is not eroded so deeply that the ornamental layer is completely removed.

5) Ornament or lack of ornament of the intexine.

6) The size range of grains falling within any one species, which, although variable, is useful in specific determination provided enough specimens are available to determine size-variation ranges accurately.

OCCURRENCE AND POSSIBLE DEPOSITIONAL ENVIRONMENT

Grains assignable to the genus *Classopollis* have been recorded from almost every microfloral assemblage of Jurassic or Lower Cretaceous age, in varying abundance. At some horizons, particularly in the Jurassic, it occurs in considerable abundance and is frequently dominant. It may, in rare cases, constitute up to 98% of the entire assemblage. These assemblages, rich in *Classopollis*, frequently carry a very characteristic microflora containing, in addition to *Classopollis*, a moderate abundance of inaperturate pollen, fairly abundant Monosulcites, and a varying, but usually small, percentage of trilete spores. Conifer pollen is always scarce and frequently very rare or absent. Marine microflora is never abundant, but a small percentage of Dinophyceae and Hystrichospheridea are present in a

majority of the assemblages. Lithologically, samples rich in *Classopollis* are usually soft, light gray, gray-green, or brown shales or mudstones of the type deposited in shallow water. Strata carrying assemblages of this type frequently grade laterally in one direction into strata carrying predominantly marine assemblages and in the other into strata with assemblages rich in Monosulcites-type pollen. Since *Classopollis*-type pollen is obviously not of a nature that would be carried over great distances, it is reasonable to assume that almost pure thickets of the plant must have occurred in areas where *Classopollis* pollen makes up the bulk of the spore and pollen spectrum. Both the occurrence of marine microflora and the predominant lithology of the deposits containing the species in abundance suggest that the plants producing *Classopollis* pollen favored a coastal environment. The rarity of conifer pollen and trilete spores in such assemblages, together with the abundance of Monosulcites, probably derived from the Cycadaceae in laterally adjacent areas, suggests dry climatic conditions. Thus, it appears probable that an abundance of *Classopollis* pollen in a sample indicates that it was deposited in a coastal region under dry climatic conditions, a conslusion which is in accord with available geologic evidence.

POSSIBLE AFFINITIES OF CLASSOPOLLIS

No Recent pollen of a type similar to *Classopollis* has been recorded, and therefore the only certain manner by which it can be related to its parent plant is by the discovery of sporangia containing grains assignable to the genus, attached to identifiable megafloral parts. Such a discovery has not yet been made, and until such time, only very general conclusions regarding its affinities can be made.

The general structure of the pollen grains, in particular the inverse tectate and internal caniculate structure of the exoexine, indicates gymnospermous affinity. This conclusion has been accepted by most authors. The opinion of Pflug and some other workers that the grains show angiospermous characters is generally not accepted, as it is based upon misinterpretation of the structure of these grains.

Hoerhammer (1933) obtained well-preserved grains assignable to the genus *Classopollis* from male cones with similar cuticular structure to and associated with *Cheirolepis muensteri* Schenk. Since these cones were not actually attached to identifiable fragments of *Cheirolepis*, the association of *Classopollis* pollen with the species *C. muensteri* cannot be regarded as proven, but despite this element of uncertainty, Hoerhammer's data provide the most significant evidence regarding the affinity of *Classopollis* currently available. Couper (1958, p. 130) recorded grains of *Classopollis* type, "very similar to those of *Pagiophyllum connivens*," associated with *Cheirolepis muensteri* in the Lower Jurassic of Wales. In that case, however, the grains were dispersed in the rock carrying the megafloral remains and were not obtained from sporangia. (These grains showed a tendency to lose their ornamented outer coat.)

Reissinger (1950) and Rogalska (1954) also assigned *Classopollis*-type pollen grains to the Cheirolepidae but provided no additional evidence for such an assignment. The record of *Classopollis* grains attached to a male cone axis associated with but not attached to remains of *Brachyphyllum scottii* Kendall (Kendall, 1949) is not as reliable as that of Hoerhammer, since only one isolated cone axis was recorded, and the cuticular structure, although similar, was not identical with that

PLATE 1

1–9 *Classopollis classoides* Pflug. 1, tetrad of grains, and 2, an enlarged view of an isolated grain, from one of Pflug's slides; 3, tetrad, and 4, enlarged view of an isolated grain, from a Canadian Jurassic sample; 5, distorted grain showing spurious tricolpate structure; 6–7, *Classopollis* cf. *classoides*, diagram (fig. 6) and photograph (fig. 7) of a specimen illustrating the proximal and distal structures; 8, tetrad, and 9, enlarged view of an isolated grain, extremely well preserved, showing details of structure.

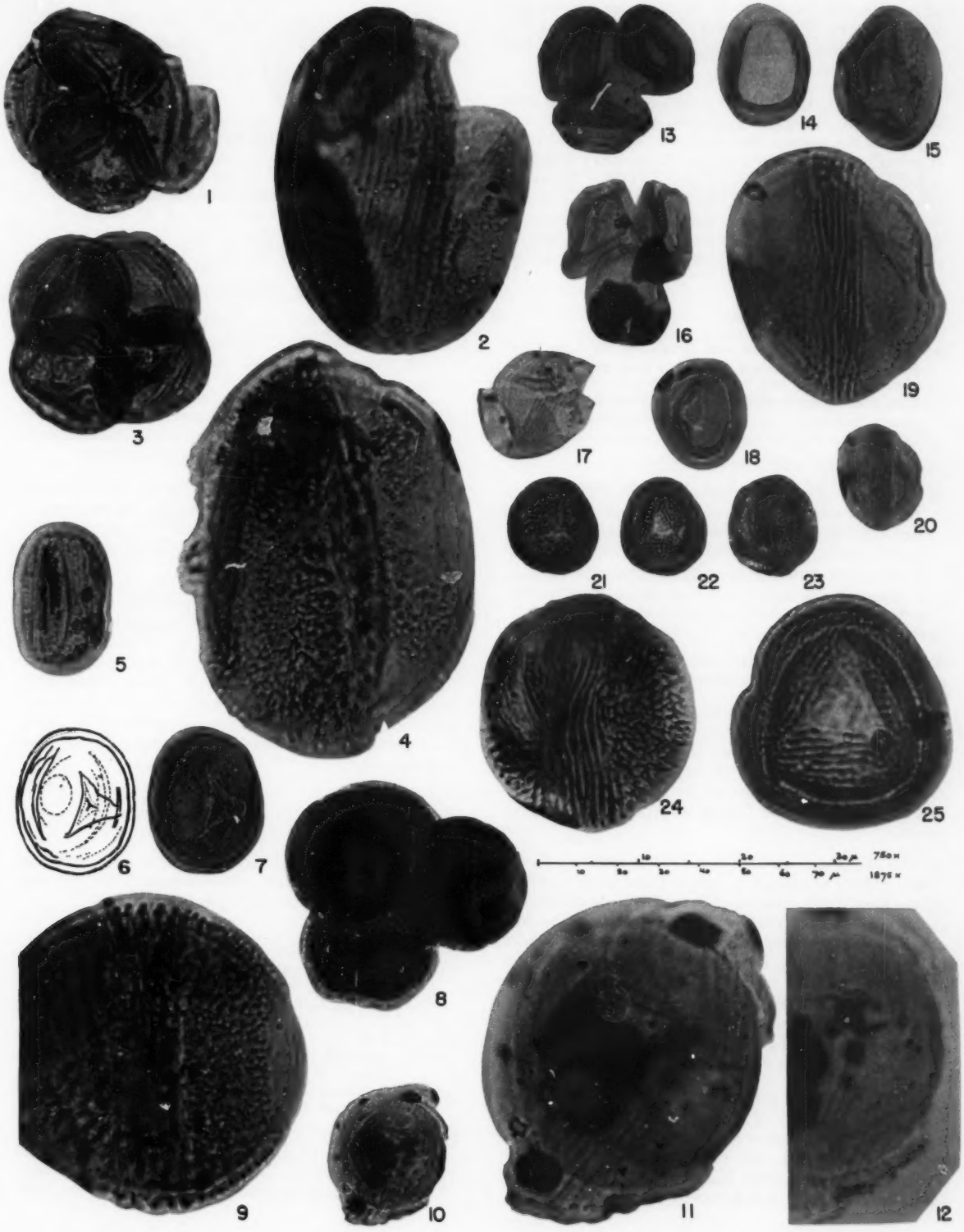
10–12 *Classopollis belloyensis* Pocock and Jansonius, n. sp. 10, equatorial view of holotype; 11–12, enlargements showing structural detail.

13 *Pollenites torosus* Reissinger. Original figure, after Reissinger (1950, pl. 14, fig. 20).

14–15 *Bennettiteae-Pollenites reclusus* Thiergart. Original figures, after Thiergart (1949): 14, Thiergart's pl. 3, fig. 6; 15, Thiergart's pl. 2, fig. 15.

16–20 *Classopollis pflugii* Pocock and Jansonius, n. sp. 16, tetrad of folded grains; 17, loose exoexinal coat (central intexinal body missing); 18, distal polar view of grain; 19–20, holotype: 19, enlarged view; 20, equatorial view.

21–25 *Classopollis minor* Pocock and Jansonius, n. sp. 21, distal polar view; 22, proximal polar view; 23, equatorial view of holotype; 24, enlarged equatorial view of holotype; 25, enlarged proximal view.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of fragments belonging to *B. scottii*. Zauer and Mchedlishvili (1954) cited Kendall's evidence in assigning *Classopollis* grains to the genus *Brachyphyllum* but provided no further evidence.

Couper (1955, 1958) re-examined grains from a cone attributed to *Pagiophyllum connivens* Kendall (1952) and expressed the opinion that they are "comparable in all respects" with *Classopollis torosus* (Reissinger), which he regards as synonymous with *C. classoides* Pflug. However, since he admitted that these grains were not clearly displayed, and as he based most of his description on dispersed *Classopollis* grains from the same stratum from which the cone was obtained, his evidence is unconvincing.

Thus, it would appear that:

a) *Classopollis*-type pollen was produced by a plant of gymnospermous affinity which is now extinct.

b) *Classopollis*-type pollen may have been produced by plants belonging to the genera *Cheirolepis*, *Brachyphyllum*, or *Pagiophyllum*, the first-mentioned genus appearing to be the most probable.

c) Since the genera *Cheirolepis* and *Brachyphyllum* are probably related, and some species of *Pagiophyllum* are difficult to distinguish from *Brachyphyllum* (Seward, 1919), it is possible that some species of all three genera produced *Classopollis*-type pollen.

ADDENDA

Since completion of the manuscript the following points have come to the authors' attention:

1) The generic name *Tetradopollenites* Sittler 1954 is a homonym of *Tetradopollenites* Pflug and Thomson 1953; its genotype *T. ericius* (Pot.) Pfl. & Th. is an angiospermous pollen. This invalidates Sittler's use of the name, and makes its use by Klaus (1960, p. 164) as a new infraturma for *Classopollis* type grains inappropriate.

2) The genus *Classopollis* Pflug 1953 is cited by Klaus (1960, p. 167) as a junior synonym of the genus *Corollina* Maljavkina 1949, emend. Klaus 1960. Maljavkina's diagnosis (1949, p. 124), which also stands as the description of the genotype *C. compacta*, describes spherical pollen grains 25–50μ in diameter with a central body and a, presumably, rather loosely fitting thick walled exoexine which may be either "spotted" or "finely veined" and is slightly thickened around the equator. The figures (pl. 46, figs. 10,11, here reproduced) do not clarify or add to the diagnostic description.

Although *Corollina* is published in accordance with the International Code of Botanical Nomenclature, it lacks the detail necessary to allow assignment of further specimens to it with any degree of certainty. In his emendation of the genus Klaus (1960, p. 167) elects Maljavkina's fig. 10 as holotype, but actually bases his

TEXT-FIGURE 6

his precise and very clearly formulated diagnosis on the figured specimens of *Classopollis* cf. *C. torosus* (Reiss.) Balme (1957, pl. 11, figs. 119–121) which are called co-types ("Hilfstypen").

The validity of this emendation is doubtful, because:

a) it is not in accord with article 36 of the International Code, in that the cited figure of the genotype does not show the essential characters of the emended genus;

b) the emended diagnosis is based upon detailed description of co-types which are not admissable for purposes of establishing taxonomic validity;

c) it cannot be demonstrated with reasonable certainty that the genotype cited corresponds with the emended diagnosis; from examination of the original diagnosisand figures there is justification in believing that it does not.

The authors feel that Klaus' emendation of *Corollina* does not invalidate the genus *Classopollis* Pflug 1953. In this connection they want to draw attention to recommendation PB6F in the International Code: "Palaeobotanists should exercise great caution in applying to well preserved specimens names which have been originally attached to poorly preserved specimens or to specimens which have been inadequately described and figured."

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ABSTRACT

Fifteen species of planktonic foraminifera are recorded from the middle Tertiary rocks of Puerto Rico. It is concluded that the two areas of outcrop of these rocks represent roughly contemporaneous successions which are lower to middle Miocene in age. The significance of two miogypsinid species is briefly considered.

Planktonic foraminifera and the correlation of the middle Tertiary rocks of Puerto Rico

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INTRODUCTION

Middle Tertiary rocks crop out over much of the north and south coastal plains in Puerto Rico. The mountainous central part of the island, composed of Cretaceous and earliest Tertiary strata, separates the middle Tertiary outcrop into two non-contiguous areas which have different stratigraphic successions. Therefore, the problem of dating the Puerto Rican middle Tertiary formations involves correlating the two principal island outcrops with each other as well as with standard successions overseas.

The northern middle Tertiary rocks of the island have been subdivided by Zapp, Bergquist, and Thomas (1948) as follows:

Aymamón limestone
Aguada limestone
Cibao marl
Lares limestone
San Sebastián formation } Río Guatemala group

The members of the Río Guatemala group were considered to be, in part, facies equivalents of each other. The same authors made the following subdivisions of the southern middle Tertiary:

Upper member
Lower member } Ponce limestone
Juana Díaz formation

The San Sebastián and Juana Díaz formations are broadly similar units which consist largely of pebble beds, clays, and marls. In both the north and the south, the higher formations are mostly limestones which continue with little interruption to the top of the succession. The faunas of the northern and southern middle Tertiary are remarkably different from each other, and comparatively few species of benthonic organisms are common to both areas. The planktonic foraminifera are the most cosmopolitan group in these rocks, and they have proved to be the most useful index fossils available.

In order to simplify the problem of correlation, the distribution of planktonic foraminifera has been studied from two sections where the northern and southern series respectively are close to their points of maximum thickness (text-fig. 1). The northern section lies between the towns of San Sebastián and Isabela where not less than 3650 feet of middle Tertiary sediments are present, and the southern section is just west of Ponce where there are perhaps 4500 feet of middle Tertiary beds. Planktonic foraminifera are distributed sporadically throughout the rocks of the northern section and become abundant in the higher part of the Aymamón limestone. In the south, they are common at all levels except the lower part of the upper Ponce limestone. Altogether, fifteen species were found.

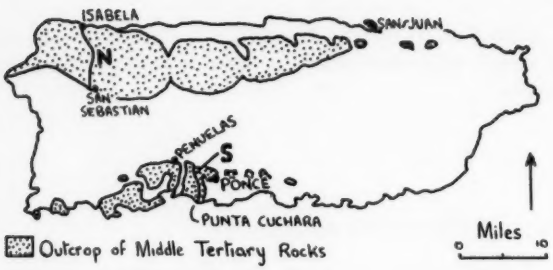
The classification of the planktonic foraminifera which is used in the following section is that of Banner and Blow (1959).

SYSTEMATIC DESCRIPTIONS

Superfamily GLOBIGERINACEAE
Family GLOBIGERINIDAE Carpenter, 1862
Genus ORBULINA d'Orbigny, 1839

Orbulina suturalis Bronnimann
Plate 1, figure 1

Orbulina suturalis BRONNIMANN, 1951, Cushman Found. Foram. Res., Contr., vol. 2, pt. 4, p. 135, text-fig. 2, figs. 1–2, 5–8, 10; text-fig. 3, figs. 3–8, 11, 13–16, 18, 20–22; text-fig. 4, figs. 2–4, 7–12, 15–16, 19–22. – WEISS, 1955, Micropaleontology, vol. 1, no. 4, p. 312, pl. 3, fig. 26. – BLOW, 1956, Micropaleontology, vol. 2, no. 1, p. 66, text-fig. 2, nos. 5–7. – BOLLI, 1957, U.S Nat. Mus., Bull. 215, p. 115, pl. 27, fig. 4.



TEXT-FIGURE 1

Sketch map of the outcrops of middle Tertiary rocks in Puerto Rico. N = location of northern section. S = location of southern section.

This species is fairly common in the Aymamón limestone and the lower Ponce limestone. Blow (1956) considered that the name *Orbulina suturalis* should be restricted to forms in which the apertural pores are confined to the sutural positions and are not distributed over the area of the last chamber.

Orbulina universa d'Orbigny
Plate 1, figure 3

Orbulina universa D'ORBIGNY, 1839, Hist. Phys. Pol. Nat. Cuba, p. 2, pl. 1, fig. 1. – GALLOWAY and HEMINWAY, 1941, New York Acad. Sci., Sci. Surv. Porto Rico and Virgin Islands, vol. 3, pt. 4, p. 414, pl. 30, fig. 3. – BERMÚDEZ, 1949, Cushman Lab. Foram. Res., Spec. Publ., no. 25, p. 282, pl. 22, fig. 3. – BLOW, 1956, Micropaleontology, vol. 2, no. 1, p. 66, text-fig. 2, nos. 8–9. – BOLLI, 1957, U.S. Nat. Mus., Bull. 215, p. 115, pl. 27, fig. 5.

This species occurs rarely in the topmost San Sebastián formation and the Lares limestone. It is common in the Aymamón limestone and the lower Ponce limestone.

Genus GLOBIGERINA d'Orbigny, 1826

Globigerina foliata Bolli
Plate 1, figure 2a–c

Globigerina pseudotriloba White. – GALLOWAY and HEMINWAY, 1941, New York Acad. Sci., Sci. Surv. Porto Rico and Virgin Islands, vol. 3, pt. 4, p. 413, pl. 29, fig. 6a–b.
Globigerina foliata BOLLI, 1957, U.S. Nat. Mus., Bull. 215, p. 111, pl. 24, figs. 1a–c.

This species is common in the Juana Díaz formation and the lower and upper Ponce limestones. It occurs sporadically in the Lares limestone and the Cibao marl.

Globigerina cf. rohri Bolli
Plate 1, figure 5a–c

cf. *Globigerina rohri* BOLLI, 1957, U.S. Nat. Mus., Bull. 215, p. 109, pl. 23, figs. 1a–4b. – BOLLI, 1957, U.S. Nat. Mus., Bull. 215, p. 164, pl. 36, fig. 4a–b.

This species is fairly common in the lower Ponce limestone of Puerto Rico. The Puerto Rican specimens differ from those described by Bolli, principally in having a very small final chamber. The range of *Globigerina rohri* in Trinidad is from the upper Eocene San Fernando formation to the *Catapsydrax dissimilis* zone (Miocene) of the Cipero formation (Bolli, 1957b). The Puerto Rican form extends into somewhat higher levels and it is probable that it should be distinguished at least as a separate subspecies.

Globigerina trilocularis d'Orbigny
Plate 1, figure 6a–c

Globigerina trilocularis D'ORBIGNY, 1826, Ann. Sci. Nat., vol. 7, p. 277, no. 2. – GALLOWAY and HEMINWAY, 1941, New York Acad. Sci., Sci. Surv. Porto Rico and Virgin Islands, vol. 3, pt. 4, p. 414, pl. 29, fig. 7a–b.
Globigerina cf. *trilocularis* d'Orbigny. – BOLLI, 1957, U.S. Nat. Mus., Bull. 215, p. 110, pl. 22, figs. 8a–9c.

This species is common in the Juana Díaz formation and the lower and upper Ponce limestones of Puerto Rico. It also occurs infrequently in the San Sebastián formation, Lares limestone, and Cibao marl, and commonly in the middle of the Aymamón limestone. It is very similar to some specimens of *Globigerinoides triloba immatura* LeRoy, but it may be distinguished from the latter by its having only one aperture.

Globigerina venezuelana Hedberg
Plate 1, figure 4a–c

Globigerina venezuelana HEDBERG, 1937, Jour. Pal., vol. 11, no. 8, p. 681, pl. 92, fig. 7. – CUSHMAN and STAINFORTH, 1945, Cushman Lab. Foram. Res., Spec. Publ., no. 14, p. 67, pl. 12, fig. 13a–b. – BERMÚDEZ, 1949, Cushman Lab. Foram. Res., Spec. Publ., no. 25, p. 280, pl. 21, figs. 39–40. – WEISS, 1955, Micropaleontology, vol. 1, no. 4, p. 310, pl. 2, figs. 18–20. – BOLLI, 1957, U.S. Nat. Mus., Bull. 215, p. 110, pl. 23, figs. 6a–8b. – BOLLI, 1957, U.S. Nat. Mus., Bull. 215, p. 164, pl. 35, figs. 16a–17. – BECKER and DUSENBURY, 1958, Cushman Found. Foram. Res., Spec. Publ., no. 4, p. 44, pl. 6, fig. 1a–b. – DROOGER and MAGNÉ, 1959, Micropaleontology, vol. 5, no. 3, pl. 1, fig. 3a–c.
Globigerina ouachitaensis Howe and Wallace. – GALLOWAY and HEMINWAY, 1941, New York Acad. Sci., Sci. Surv. Porto Rico and Virgin Islands, vol. 3, pt. 4, p. 412, pl. 29, figs. 4a–c.

This species occurs abundantly in Puerto Rico in the Juana Díaz formation, the lower and upper Ponce limestones, and the Aymamón limestone. It is rare in the top part of the Cibao marl. The Puerto Rican specimens show considerable variation in shape, but many of them are virtually identical with the holotype which was described from the Carapita formation, Oligocene, of Venezuela.

Genus GLOBOQUADRINA Finlay, 1947

Globoquadrina altispira altispira (Cushman and Jarvis)
Plate 1, figure 7a–c

Globigerina altispira CUSHMAN and JARVIS, 1936, Cushman Lab. Foram. Res., Contr., vol. 12, pt. 1, p. 5, pl. 1, figs. 13a–c, 14. – CORYELL and RIVERO, 1940, Jour. Pal., vol. 14, no. 4, p. 329, pl. 42, fig. 31. – BERMÚDEZ, 1949, Cushman Lab. Foram. Res., Spec. Publ., no. 25, p. 277, pl. 21, fig. 43. – WEISS, 1955, Micropaleontology, vol. 1, no. 4, p. 310, pl. 3, figs. 1–3.

Globigerina pachyderma (Ehrenberg). – GALLOWAY and HEMINWAY, 1941, New York Acad. Sci., Sci. Surv. Porto Rico and Virgin Islands, vol. 3, pt. 4, p. 413, pl. 29, fig. 5a–c.

Globoquadrina altispira altispira (Cushman and Jarvis). – BOLLI, 1957, U.S. Nat. Mus., Bull. 215, p. 111, pl. 24, figs. 7a–8b.

In Puerto Rico this subspecies is fairly common in the Juana Díaz formation, lower Ponce limestone, and Aymamón limestone, and rare in the Lares limestone and Cibao marl. Although variable in form, many specimens are indistinguishable from the type specimen which Cushman and Jarvis described from the Miocene Bowden marl of Jamaica. The form illustrated by Weiss (1955) is not as high-spired as the typical specimens, but it appears to belong to the same subspecies

Globoquadrina altispira globosa Bolli

Globoquadrina altispira globosa BOLLI, 1957, U.S. Nat. Mus., Bull. 215, p. 111, pl. 24, figs. 9a–10c.

A few specimens in the lower part of the lower Ponce limestone of Puerto Rico are placed in this subspecies. They have only four chambers in the last whorl and are transitional in shape toward *Globoquadrina altispira altispira* (Cushman and Jarvis). The typical members of subspecies *globosa* are described by Bolli (1957*a*) as having 5–6 chambers in the last whorl.

Genus GLOBIGERINOIDES Cushman, 1927

Globigerinoides triloba immatura LeRoy
Plate 2, figure 1a–c

Globigerinoides sacculifer (Brady). – CUSHMAN and STAINFORTH, 1945, Cushman Lab. Foram. Res., Spec. Publ., no. 14, p. 68, pl. 13, fig. 3.

Globigerinoides triloba immatura LeRoy. – BOLLI, 1957, U.S. Nat. Mus., Bull. 215, p. 113, pl. 25, figs. 3a–4c, text-fig. 21, no. 2.

In Puerto Rico this species is common in the Juana Díaz formation and the lower and upper Ponce limestones. It occurs rarely in the San Sebastián formation, Cibao marl, and Aymamón limestone.

Globigerinoides sp.

Five badly preserved specimens in the lower Ponce limestone appear to belong to an undescribed species of *Globigerinoides*, but there is insufficient material available at present on which to erect a new species.

Genus SPHAEROIDINELLOPSIS Banner and Blow, 1959

This genus is distinguished from *Sphaeroidinella* Cushman, 1927, emend. Banner and Blow, 1959, by its lack of supplementary sutural apertures in the adult. Banner and Blow (1959) consider that it is ancestral to *Sphaeroidinella*, and that its stratigraphic range is from lower to upper Miocene.

Sphaeroidinellopsis rutschi (Cushman and Renz)
Plate 2, figure 4a, b

Sphaeroidinella rutschi CUSHMAN and RENZ, 1941, Cushman Lab. Foram. Res., Contr., vol. 17, pt. 1, p. 25, pl. 4, fig. 5. – BOLLI, 1957, U.S. Nat. Mus., Bull. 215, p. 115, pl. 26, figs. 6a–7b.

This species is fairly common in the higher part of the lower Ponce limestone and the upper Ponce limestone of Puerto Rico.

Sphaeroidinellopsis seminulina (Schwager)
Plate 2, figure 6a–c

Sphaeroidinella seminulina (Schwager). – GALLOWAY and HEMINWAY, 1941, New York Acad. Sci., Sci. Surv. Porto Rico and Virgin Islands, vol. 3, pt. 4, p. 415, pl. 30, fig. 4a–b.

In Puerto Rico this species occurs infrequently in the uppermost Aymamón limestone. The Puerto Rican specimens seem to be indistinguishable from topotype specimens in the United States National Museum which are labeled "from Schwager's material." The species was described by Schwager (1866) from the Pliocene of Kar Nicobar, India.

Genus GLOBOROTALIA Cushman, 1927

Globorotalia menardii (d'Orbigny)
Plate 2, figure 3a–c

Rotalia menardii D'ORBIGNY, 1826, Ann. Sci. Nat., vol. 7, p. 273, no. 26, modèle no. 10.

Globorotalia menardii (d'Orbigny). – CORYELL and RIVERO, 1940, Jour. Pal., vol. 14, no. 4, p. 336, pl. 42, figs. 34–35. – GALLOWAY and HEMINWAY, 1941, New York Acad. Sci., Sci. Surv. Porto Rico and Virgin Islands, vol. 3, pt. 4, p. 368, pl. 16, figs. 5a–c. – WEISS, 1955, Micropaleontology, vol. 1, no. 4, p. 312, pl. 3, figs. 21–23. – BOLLI, 1957, U.S. Nat. Mus., Bull. 215, p. 120, pl. 29, figs. 6a–10b.

In Puerto Rico this species occurs infrequently in the Cibao marl and the Aymamón limestone. The Puerto Rican specimens are usually not as compressed as most forms which have been referred to this species, but they are less strongly biconvex than the related form, *Globorotalia menardii* var. *tumida* (Brady).

Genus GLOBOROTALOIDES Bolli, 1957

Globorotaloides variabilis Bolli
Plate 2, figure 2a–c

Globorotaloides variabilis BOLLI, 1957, U.S. Nat. Mus., Bull. 215, p. 117, pl. 27, figs. 15a–20c, particularly figs. 17a–19c.

This species is common in the Juan Díaz formation, lower and upper Ponce limestones, and Aymamón limestone of Puerto Rico. It is rare in the Cibao marl.

Genus HASTIGERINA Thomson, 1876

Hastigerina cf. siphonifera (d'Orbigny)

Plate 2, figure 5a–c

cf. *Globigerina siphonifera* D'ORBIGNY, 1839, Hist. Phys. Pol. Nat. Cuba, p. 83, pl. 4, figs. 15–18.

Globigerinella aequilateralis (Brady). – BERMÚDEZ, 1949, Cushman Lab. Foram. Res., Spec. Publ., no. 25, p. 280, pl. 21, fig. 51.

Hastigerina cf. *aequilateralis* (Brady). – BOLLI, 1957, U.S. Nat. Mus., Bull. 215, p. 108, pl. 22, figs. 1a–2b, especially 1a–c.

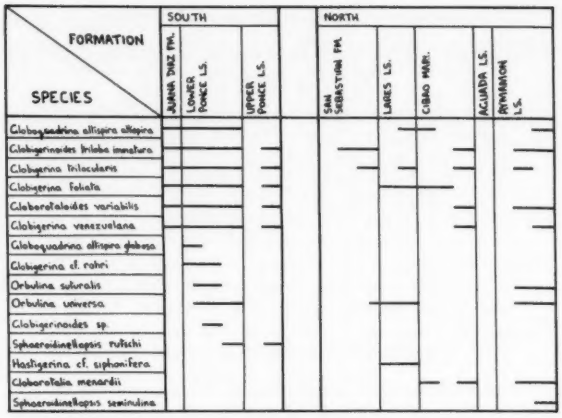
cf. *Hastigerina (Hastigerina) siphonifera* (d'Orbigny). – BANNER and BLOW, 1960, Micropaleontology, vol. 6, no. 1, p. 22, text-figs. 2a–c, 3a, b.

In Puerto Rico this species is rare in the Lares limestone The Puerto Rican specimens are not well preserved, but they seem to be indistinguishable from those of Bolli (1957*a*) from the Lengua formation, Miocene, of Trinidad. The specimens of Bermúdez (1949) from the Gurabo and Mao formations, Miocene, of the Dominican Republic are also very similar. Banner and Blow (1960) selected a lectotype of *Globigerina aequilateralis* Brady from a syntypic series of Brady's specimens, and they stated that this specimen is "virtually identical in all respects" to the lectotype of *Globigerina siphonifera* d'Orbigny, also selected by Banner and Blow. *Globigerina aequilateralis* Brady is therefore a synonym of *Globigerina siphonifera* d'Orbigny, and so it is preferred to compare the Puerto Rican specimens to d'Orbigny's form rather than to Brady's. The Puerto Rican specimens are more compressed and more evolute than d'Orbigny's form, and the chambers are less globose. It is probable that a new species will have to be erected for the Caribbean Miocene forms when adequate material becomes available.

CORRELATION OF THE MIDDLE TERTIARY ROCKS

The Puerto Rican middle Tertiary rocks were considered by Berkey (1915) as possibly ranging in age from Eocene to Miocene. Subsequent authors (Hubbard, 1920, 1923; Maury, 1929; Meyerhoff, 1933; Galloway and Heminway, 1941; and Woodring, 1943) thought that the rocks of the north coast outcrop are either middle or upper Oligocene to upper Oligocene or, more usually, lower Miocene. Coryell and Ohlsen (1929) concluded from a study of the coral faunas that they range from middle Oligocene to middle Miocene. More recent investigations by Zapp, Bergquist, and Thomas (1948) produced the conclusion that their age is middle Oligocene to lower Miocene.

With regard to the south coast outcrops, most workers have agreed that these sediments are the approximate time equivalents of the northern sequence. Woodring (1943, chart) differed slightly from other authors in suggesting that the southern deposits may commence later and finish earlier than the northern middle Tertiary.

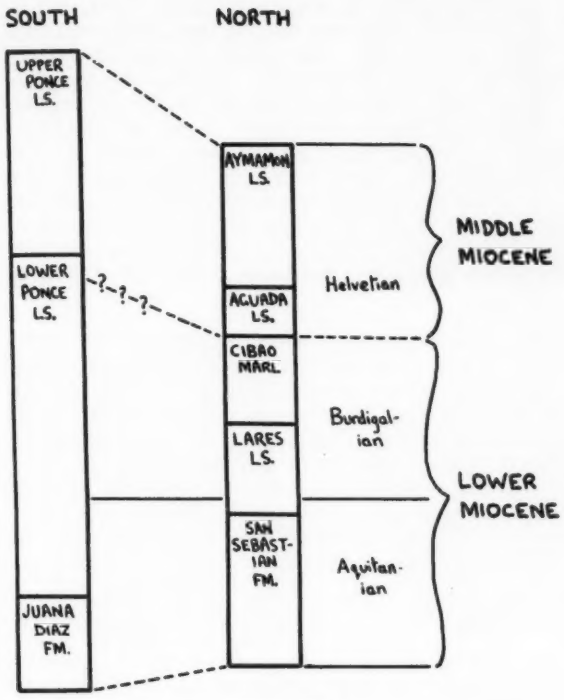


TEXT-FIGURE 2

Distribution of planktonic foraminifera in the middle Tertiary rocks of Puerto Rico.

Until recently, it has appeared that the correlations proposed by Zapp, Bergquist, and Thomas for the Puerto Rican middle Tertiary were generally satisfactory. However, there has been much controversy in the literature of the Caribbean Oligo-Miocene rocks in the last few years, and new evidence has shown that the correlation of the Puerto Rican strata must be re-examined in the light of more recent knowledge. Eames (1953) cast doubt on the status of the rocks which have been referred to the Oligocene in the Caribbean region, and he advocated the use of *Orbulina* and *Miogypsina* as evidence of a post-Oligocene age in the rocks in which they occur. In subsequent correspondence in the Geological Magazine, Stainforth (1954) disagreed with Eames, but the latter wrote (Eames, 1954) in reply to emphasize that the terms Oligocene, Miocene, and Aquitanian had been defined from European localities, and that it was necessary to re-examine the Caribbean paleontological evidence from the beginning and to make correlations taking into account the evidence from the rest of the world. Kugler (1954) stated that the top of the Oligocene had previously been placed too high in Trinidad, and that the *Globorotalia fohsi* zone belongs in the lower Miocene, not the upper Oligocene. He temporarily placed the Oligocene-Miocene boundary at the base of the *fohsi* zone, but left open the possibility that beds bearing *Miogypsina s. str.* below this zone may belong to the Miocene also. Eames (1955) went farther than Kugler in suggesting that the whole of the Cipero formation of Trinidad is of lower Miocene rather than upper Oligocene age.

Drooger (1956) placed the Oligocene-Miocene boundary between the *Globigerina ciperoensis* and *Catapsydrax dissimilis* zones of Trinidad, but Eames and Clarke (1957) disagreed with this conclusion. They reviewed evidence from the Mediterranean area and the Middle East which showed that Drooger had placed the base of the Miocene a little too high on his correlation chart.



TEXT-FIGURE 3

Correlation of the middle Tertiary rocks of Puerto Rico.

They also stated that *Orbulina suturalis* Bronnimann and *Orbulina universa* d'Orbigny range down into the upper Aquitanian, and that *Orbulina* occurs in the same beds as *Miogypsinoides complanata* (Schlumberger) at several localities known to them. Drooger had considered *M. complanata* to be a pre-Aquitanian species, but Eames and Clarke said that it occurs also in "undoubted Aquitanian (basal Miocene)" rocks.

It appeared that the correlation of the Puerto Rican middle Tertiary formations might well need revision. Accordingly, a study of the planktonic and other foraminifera was made and it was seen at once that previous correlations would have to be discarded. Even at the generic level, four of the eight genera of planktonic foraminifera which were found in these rocks suggested that most of the sediment is Miocene in age. The following ranges for genera which occur in Puerto Rico were given by Banner and Blow (1959) in their revision of the Globigerinaceae: *Orbulina*, lower Miocene—Recent; *Globoquadrina*, Aquitanian—Pliocene; *Sphaeroidinellopsis*, lower—upper Miocene; and *Hastigerina*, lower Miocene —Recent.

Probably the best datum to use in correlating the Puerto Rican rocks is the first appearance of *Orbulina universa* in the topmost part of the San Sebastián formation and of *O. universa* and *O. suturalis* in the lower Ponce limestone. The writer has shown that the first appearance of *Orbulina universa* in the San Sebastián is close to its first possible appearance (Gordon, 1960, in press), and it is thought likely that the same is true of the occurrence of *Orbulina* in the lower Ponce limestone. This is because reasonably good faunas of planktonic foraminifera were obtained from rocks lower down in the succession, but no *Orbulina* was found.

The importance of the first appearance of *Orbulina* as a world datum was suggested by LeRoy (1948) and Tromp (1949), and many later authors have agreed with them on its significance. These include Hornibrook (1958), who pointed out that the evolutionary series which leads to *Orbulina* has been recorded from the Central American region (Blow, 1956), the Mediterranean (Blow, 1957), and New Zealand (Finlay, 1947), indicating that *Orbulina* did not evolve in one area and migrate at a later period into other regions. Bowen (1955) concluded that all pre-Miocene records of *Orbulina* are probably to be considered either as cases of mistaken identity or of mistaken correlations of the sediments in which they occur. Eames and Clarke (1957), Blow (1957), Hornibrook (1958), and Banner and Blow (1959) all agreed that *Orbulina* ranges from the upper Aquitanian upward. The distribution of *Orbulina universa* and *O. suturalis* in Puerto Rico suggests, therefore, that the top of the Aquitanian stage coincides with, or is slightly higher than, the top of the San Sebastián formation in the northern succession. In the south, the Aquitanian-Burdigalian boundary is considered to fall within the lower Ponce limestone.

The age of the rocks below the earliest occurrence of *Orbulina* can be determined most satisfactorily on the south coast of Puerto Rico. Here, *Globoquadrina altispira altispira* (Cushman and Jarvis), a good Miocene index fossil, occurs from low in the Juana Díaz formation to the top of the lower Ponce limestone. In Trinidad, this form ranges down only as far as the *Catapsydrax stainforthi* zone and it is therefore well within strata which Bolli (1957*a*) regarded as Miocene. If Blow (1957) is correct in placing "at least a part of the *Globigerina ciperoensis*" zone of Trinidad in the Miocene, then the first appearance of *Globoquadrina altispira altispira* is even higher above the base of the system. It follows that even the lowest beds of the south coast middle Tertiary of Puerto Rico are probably Miocene. It has already been suggested that the northern middle Tertiary sequence is entirely Miocene (Gordon, 1960), and on general structural grounds it is reasonable to suppose that sedimentation began roughly contemporaneously on the north and south sides of Puerto Rico after the early Tertiary interval of nondeposition. There is, however, no good fossil evidence to confirm this assumption.

It is not possible to make a very precise correlation of the higher middle Tertiary formations. The presence

of a few specimens of *Globorotalia menardii* (d'Orbigny) in the northern sediments from the lower part of the Cibao marl upward indicates that the higher Cibao and later beds are probably equivalent to the *Globorotalia mayeri* and *Globorotalia menardii* zones of Trinidad and possibly also to later horizons. *Globoquadrina altispira altispira* is abundant in the highest part of the Aymamón limestone, and this may be an indication that the whole of the formation is not younger than the middle Miocene. *G. altispira altispira* does not seem to be known from the upper Miocene, although its type horizon, the Bowden marl of Jamaica, is possibly of this age. Blow (1957), from a review of evidence seen in Malta and Sicily, considered that the Burdigalian-Helvetian boundary probably coincides with the top of the *Globorotalia mayeri* zone of Trinidad and, if this is so, the boundary between these two stages in northern Puerto Rico may fall somewhere fairly close to the junction of the Cibao marl and the Aguada limestone. That is, fairly soon after the first appearance of *Globorotalia menardii* in these rocks.

On the south coast, *G. altispira altispira* is never abundant and it is missing entirely above the lower Ponce limestone. Its absence from the higher beds is probably related to the general decline in the numbers of the planktonic foraminifera in the upper Ponce limestone rather than to extinction of the form. *Sphaeroidinellopsis rutschi* occurs sporadically from the upper part of the lower Ponce limestone to the top of the succession, and reference to its distribution in Trinidad (Bolli, 1957*a*, table) suggests that the Puerto Rican rocks in which it occurs are not older than the base of the *Globorotalia mayeri* zone of Trinidad. Once again, if the contention of Blow (1957) that the top of the *mayeri* zone is probably equivalent to the Burdigalian-Helvetian boundary is correct, this junction falls near the top of the lower Ponce limestone in Puerto Rico.

With respect to the age of the topmost strata of the southern middle Tertiary rocks of the island, it is possible at present to say only that the composition of the fauna has a broadly middle Miocene appearance. The benthonic foraminiferal fauna of the highest Ponce limestone is similar to that of the top of the Aymamón limestone, and the two deposits are considered to be fairly contemporaneous.

MIOGYPSINIDS IN PUERTO RICO

Apart from the planktonic foraminifera, miogypsinids provide the most significant index fossils in the Puerto Rican middle Tertiary. Two species are known by the writer to occur in Puerto Rico. *Miogypsinoides complanata* (Schlumberger) occurs in the northern section in the topmost San Sebastián formation and the basal Lares limestone, and it occurs in the south in the lower part of the lower Ponce limestone. *Miogypsinoides bermudezi* (Drooger) is found in the northern section near the middle of the San Sebastián formation.

The range of *Miogypsinoides complanata* has been the subject of controversy in recent years. It was considered an upper Oligocene marker fossil by Drooger (1954, 1956), Akers and Drooger (1957), and Drooger and Magné (1959). From evidence in the Mediterranean region, Blow (1957) stated that it ranges into the Aquitanian, and Eames and Clarke (1957) agreed with this conclusion, adding that *Miogypsinoides complanata* and *Orbulina* occur together in the Mediterranean and elsewhere. It therefore seems impossible to doubt that this species ranges well above the top of the Oligocene. In Puerto Rico, *Miogypsinoides complanata* occurs in beds which are just above the lowest occurrence of *Orbulina universa*.

Miogypsinoides bermudezi was described by Drooger (1951) from a well at Baños, Pinar del Río Province, Cuba, from beds which he considered to be early middle Oligocene. Until now, it does not seem to have been reported from any other locality, but its occurrence in Puerto Rico suggests that it is either a long range form or that the type horizon is in reality younger than at first appeared to be the case. When its range is better known, *Miogypsinoides bermudezi* may well prove to be a most useful index form.

CONCLUSIONS

The middle Tertiary rocks of Puerto Rico, as seen in two sections where the northern and the southern series respectively are at their maximum development, are considered to be wholly Miocene in age (text-figure 3).

PLATE 1

All figures × 90, except figures 4a–5c, × 60

1 *Orbulina suturalis* Bronnimann
Apertural view. Aymamón limestone.

2 *Globigerina foliata* Bolli
a, spiral view; b, side view; c, umbilical view. Lower Ponce limestone.

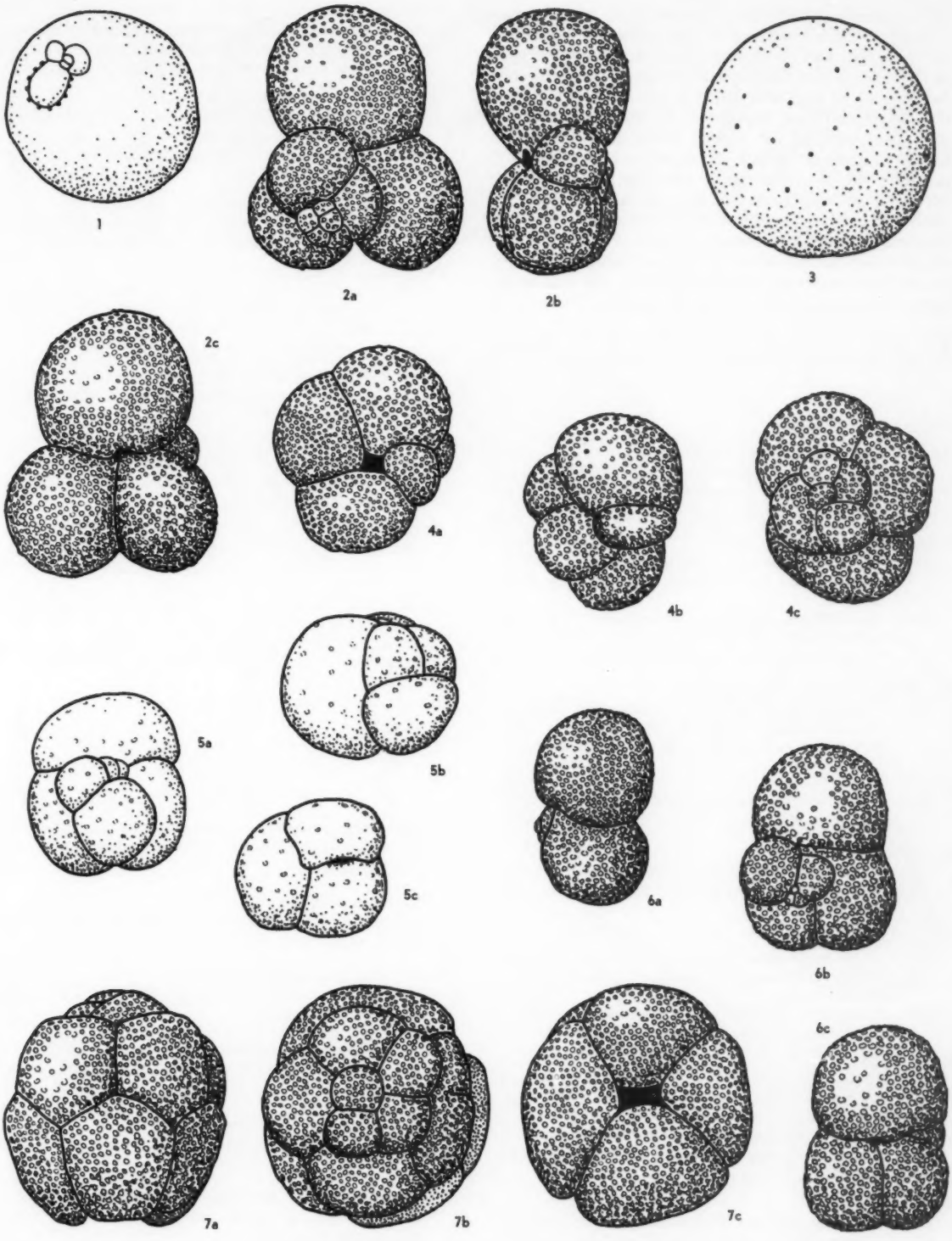
3 *Orbulina universa* d'Orbigny
Aymamón limestone.

4 *Globigerina venezuelana* Hedberg
a, umbilical view; b, side view; c, spiral view. Lower Ponce limestone.

5 *Globigerina* cf. *rohri* Bolli
a, spiral view; b, side view; c, umbilical view. Lower Ponce limestone.

6 *Globigerina trilocularis* d'Orbigny
a, side view; b, spiral view; c, umbilical view. Lower Ponce limestone.

7 *Globoquadrina altispira altispira* (Cushman and Jarvis)
a, side view; b, spiral view; c, umbilical view. Aymamón limestone.


1
2a
2b
3
2c
4a
4b
4c
5a
5b
5c
6a
6b
6c
7a
7b
7c

Fifteen species of planktonic foraminifera which occur in these rocks indicate that the San Sebastián formation in the north, and the Juana Díaz formation and part of the lower Ponce limestone in the south, are probably Aquitanian in age. The Lares limestone and much of the Cibao marl are thought to be Burdigalian, as is the upper part of the Lower Ponce limestone. The higher formations in both the north and the south are probably middle Miocene in age. The occurrence of *Miogypsinoides complanata* and *Miogypsinoides bermudezi* in the lower parts of the Puerto Rican successions does not invalidate these conclusions because the significance of the latter cannot as yet be assessed, and the former is now well established as an Aquitanian (as well as an upper Oligocene) fossil in several localities.

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PLATE 2
All figures × 90

1 *Globigerinoides triloba immatura* LeRoy
a, umbilical view; b, spiral view; c, side view. Lower Ponce limestone.

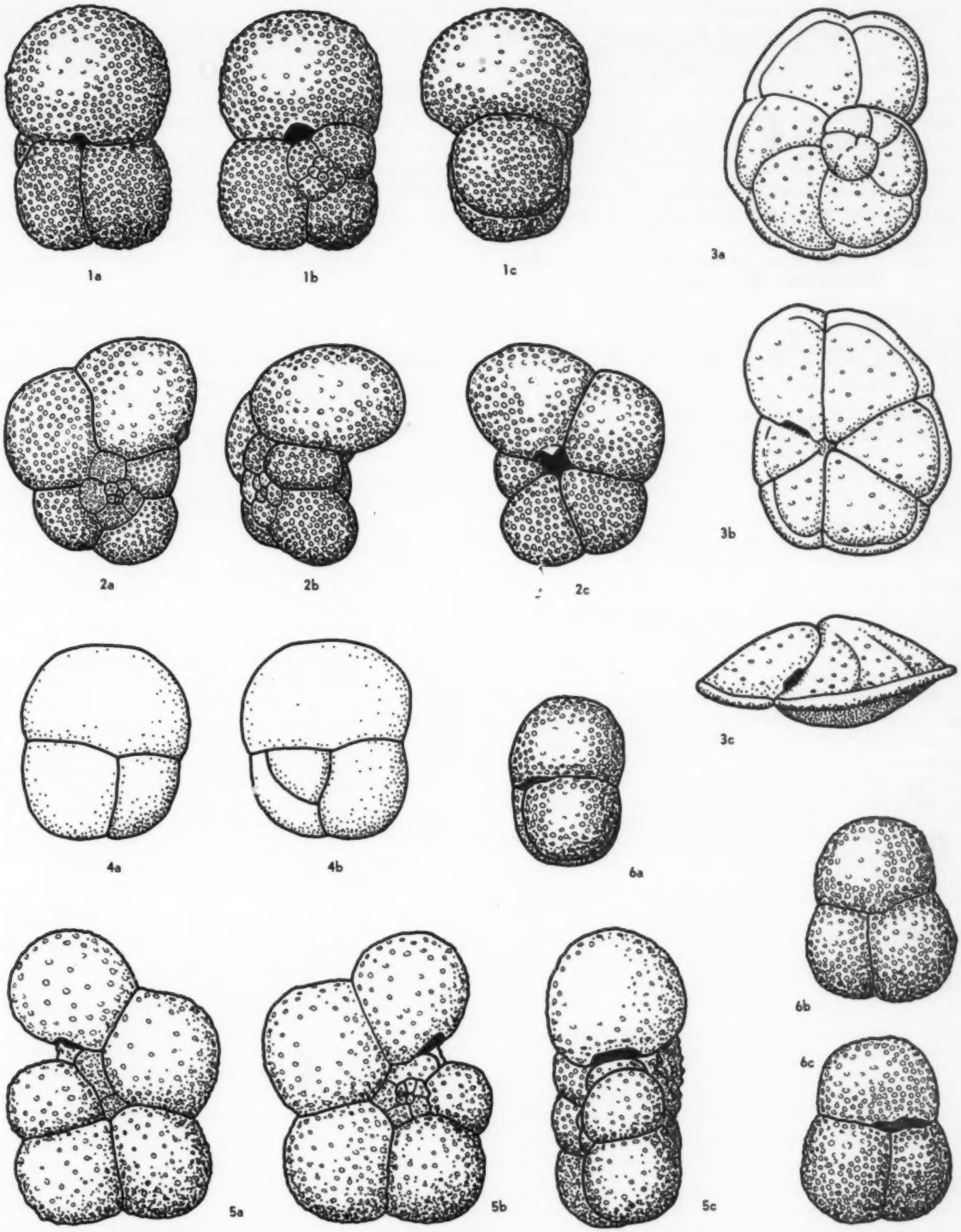
2 *Globorotaloides variabilis* Bolli
a, spiral view; b, side view; c, umbilical view. Lower Ponce limestone.

3 *Globorotalia menardii* (d'Orbigny)
a, spiral view; b, umbilical view; c, side view. Aymamón limestone.

4 *Sphaeroidinellopsis rutschi* (Cushman and Renz)
a, umbilical view; b, spiral view. Upper Ponce limestone.

5 *Hastigerina* cf. *siphonifera* (d'Orbigny)
a, umbilical view; b, spiral view; c, side view. Lares limestone.

6 *Sphaeroidinellopsis seminulina* (Schwager)
a, side view; b, spiral view; c, umbilical view. Aymamón limestone.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ABSTRACT

Methods employed for routine laboratory culture of foraminifera are described, including a method for establishing axenic or synxenic culture. Attempts have been made to grow Trochammina inflata, Miliammina fusca, Elphidium poeyanum, Allogromia sp., Quinqueloculina sp., *and* Streblus beccarii *in limited agnotobiotic and synxenic culture.*

The algae and the foraminifera have been grown and tested in enriched seawater and artificial seawater media. None of the synxenic cultures tested support continuous growth and reproduction of the foraminifera. A Mixture of eight pennate diatoms, three bacteria, and three blue-green filamentous algae supports abundant growth of Streblus beccarii *cultures.* Nitzschia acicularis *was found to stimulate the growth of* Bolivina sp.; *another species of* Nitzschia *was found to inhibit growth; and there was no response to a mixture of* Rhodomonas lens *and* Isochrysis galbana. *Reactions between* Dunaliella *cultures and foraminifera are described.*

Growth and physiology of foraminifera in the laboratory: Part 1 — Collection and maintenance

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INTRODUCTION

The secrets of living foraminifera have barely been probed, although foraminifera are easy to collect and maintain in crude laboratory cultures. Such cultures (Arnold, 1954, Myers 1935, 1937) are useful in life cycle and taxonomic studies, but, from a microbiological standpoint, nutritional-physiological studies are impossible. Part of the difficulty in establishing axenic (without any other organisms, see McLaughlin, 1960) or synxenic (where all the associated organisms are known) cultures of foraminifera has been the scarcity of correlative information.

Information on raising marine algae and protozoa has increased greatly in recent years. Extensive collections of axenic cultures of phytoplanktonts have been established; some forms have already been found to be useful as food organisms for marine larvae of economic importance (Davis and Guillard, 1958). At the same time, the exact nutritional requirements of such food organisms, and of larger marine animals, are being determined. We are applying these new techniques to the study of foraminifera.

MATERIALS AND METHODS

Collecting

Our methods of collecting and handling foraminifera are essentially those suggested by Arnold (1954) in his excellent review. Foraminifera were collected in the Toms River area of Barnegat Bay, New Jersey; at the Biological Station, Cold Spring Harbor, Long Island; at various places on the southeastern shore of Long Island in the vicinity of Westhampton Beach; and along the shores of Great and Little Peconic Bays at the eastern end of Long Island.

Cultivation

Some of the collections brought back to the laboratory were placed in a circulating marine aquarium system. Others were cultured in fingerbowls or Petri dishes, as suggested by Arnold (1954); and some foraminifera were picked and inoculated into experimental tubes on the day of collection.

Laboratory cultures are maintained at either 15° C in a B.O.D. incubator or at room temperatures of 22–25° C, which is maintained by room air conditioning. Food organisms are grown in tubes or flasks in front of banks of fluorescent lights. Illumination is regulated by a 24-hour variable time switch and position before the light bank (16–500 FC).

Forty gallons of sea water in our aquarium is circulated through the system by a Bro-jo plastic pump at an average rate of 0.5 L/min. The glass tanks, with stainless steel frames, are connected by plastic pipe.

Glass wool and charcoal are used to filter and purify the circulating water. Salinity is maintained at about 26‰ by addition of sea water obtained from the New York Aquarium, or by the addition of distilled water. The pH is adjusted to 7.8–8.1 with NaOH or HCl. As an initial step, Pasteur pipettes are used to remove the "forams" from the sand, debris, and metazoa with which field samples are contaminated.

Axenic or synxenic cultures are obtained by washing foraminifera through sterile media and by treatment with antibiotics. Small groups of foraminifera are made aseptic by isolation into screw-cap tubes of sterile sea water, and then gently agitated. These specimens are transferred into another sterile tube and agitated again. After ten serial washings, the specimens are inoculated into tubes containing chloroamphenicol 0.2 mg/ml, dihydrostreptomycin 1 mg/ml, polymyxin B 0.02 mg/ml and nystatin 0.05 mg/ml. After 48 hours, the specimens are removed from the media and washed an additional ten times. This treatment apparently does not harm our specimens as evidenced by normal pseudopodal activity and growth. Synxenic cultures are then established by inoculation of the sterile "forams" into axenic algal cultures. "Sterility" of our cultures is checked by the transfer of one or two foraminifera into tubes of marine nutrient broth, STP, DC (Provasoli *et al*, 1957), or by streaking on marine nutrient agar. Cloudiness in the liquid media or colony growth on the agar is presumed evidence of contamination. With this technique of washing – antibiotic treatment – washing 70–100% of the cultures are axenic.

Activity of the foraminifera and their associated organisms is noted through the test tube walls. This facilitates counting numbers of organisms without exposing the cultures to contamination.

It is practical to keep a number of reagents in solution. This saves time weighing small amounts and reduces potential error. Stock solutions are protected against microbial action by a preservative which is removed by steam sterilization. In general, we have used the apparatus and techniques outlined by Hutner *et al* (1958). We have also grown foraminifera with many of the synthetic marine media reported by Provasoli *et al* (1957) and Pintner and Provasoli (1958) and modifications of these media.

EXPERIMENTAL RESULTS

Food organisms

We have tried two approaches to the establishment of synxenic cultures of foraminifera. One of these has been to inoculate foraminifera into cultures of known organisms. The other has been to establish finger-bowl cultures of foraminifera isolated by removing other protozoa, metazoa, and metaphyta. The remaining associated organisms are eliminated systematically as subcultures are made. These new cultures are then checked for growth and reproduction.

We have tried to establish reproducing, limited agnotobiotic (bacterized) and synxenic cultures of *Trochammina inflata*, *Miliammina fusca*, *Elphidium poeyanum*, *Allogromia* sp., *Quinqueloculina* sp., *Peneroplis* sp., and *Streblus beccarii* var. *tepida*. The food organisms used were the following diatoms: *Amphora purpusilla* (DR V and DR IIIA), *Nitzschia frustulum* (53–M), *Nitzschia punctata* (52–M), *Nitzschia ovalis* (49–M), *Nitzschia closterium* (54–M), *Nitzschia* sp. (WHDCO), *Nitzschia acicularis* (DR VI), *Melosira* sp., *Amphora coffaeiformis* (45–M), *Achanthes brevipes* (Watson 7), *Cyclotella* sp., and *Amphiprora paludosa* var. *duplex* (73–M). The phytoflagellates tested as potential food included *Dunaliella salina*, *Dunaliella parva* (brine chlamydomonas), *Dunaliella tertiolecta* (marine chlamydomonas), *Rhodomonas lens*, *Isochrysis galbana*, *Casseopea* symbiont (dinoflagellate), *Desmonales* sp., *Monochrysis lutheri*, *Peridinium* sp. (Larch) and *Prymnesium parvum* (PCC). The potential food was inoculated into either ASP_7 (Pintner and Provasoli, 1958), Erdschreiber, or sterile filtered sea water, about a week before the experiment. During the course of some experiments, fresh media were added when the foraminifera were inoculated. None of the above food organisms was capable of consistently supporting continuous growth and reproduction of the foraminifera in either monoxenic (one associate) or limited agnotobiotic cultures.

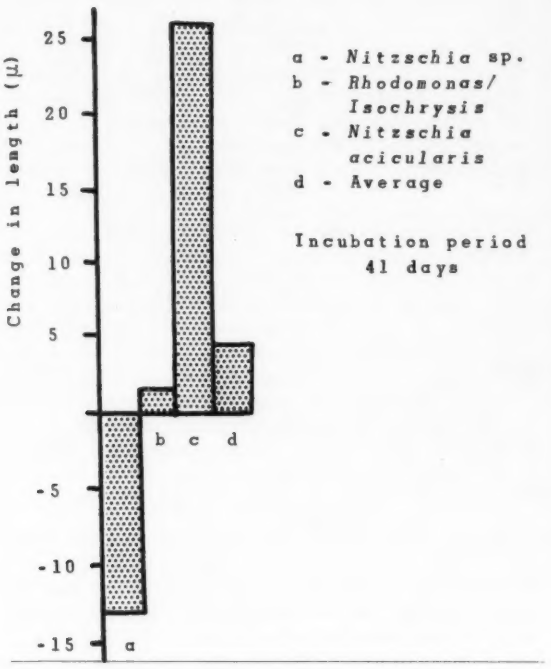
In a small pilot experiment, specimens of *Bolivina* sp. were placed in Petri dish cultures, each containing different potential food organisms. While *Nitzschia closterium*, *Nitzschia* sp. and *Amphora perpusilla* grew abundantly in the medium, they were not gathered as densely around the foraminifera as were specimens of *Nitzschia acicularis*.

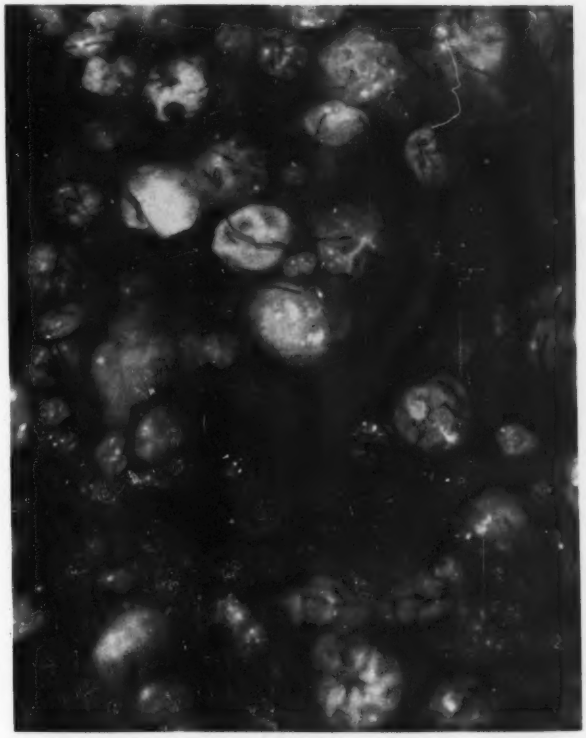
We measured the length of specimens of *Bolivina* sp. and inoculated them into Petri dish cultures of either *Nitzschia acicularis*, *Nitzschia* sp. or a mixture of *Rhodomonas lens* and *Isochrysis galbana*. These last two organisms stimulate the growth and reproduction of two crustaceans (Provasoli *et al*, 1960). Half of the cultures were incubated in subdued light (16 FC); the other half were kept in total darkness. Those incubated in the dark were fed at weekly intervals. After a six week incubation period, the total length of all specimens was again measured. In light and dark, results indicated inhibition of growth and occasional loss of terminal chambers in cultures with *Nitzschia* sp., stimulation by *Nitzschia acicularis* and neither stimulation nor inhibition by the *Rhodomonas-Isochrysis* mixture (Graph 1). There was less length increment in the dark-incubated cultures. It is possible that the amounts of available food were not equivalent.

A number of diatoms and phytoflagellates have been isolated from foraminiferal collecting environments. These isolates, when used in monoxenic or few-membered synxenic cultures, have not supported continuous growth of the foraminifera isolated from the same area. Multiple combinations of the algal isolates in synxenic culture are being tested.

GRAPH 1

GROWTH OF *BOLIVINA* SP. IN THE PRESENCE OF POTENTIAL FOOD ORGANISMS





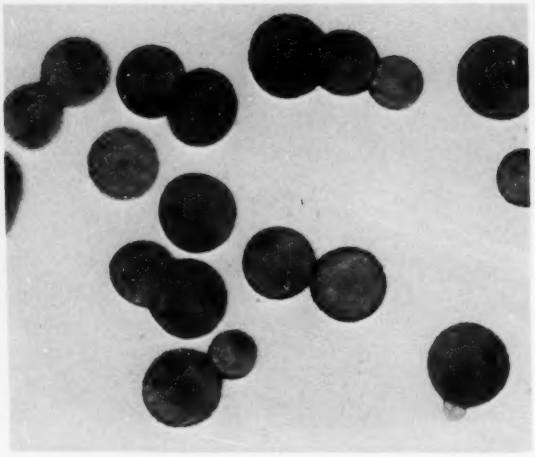
TEXT-FIGURE 1

Streblus beccarii from a 14-membered "synxenic" culture. Filaments of blue-green algae are seen on some of the foraminifera.

More promising results have been obtained by following the other line of investigation. Microscopic and bacteriological examination of the most actively growing and reproducing laboratory cultures of many species of foraminifera has revealed a common flora. (It was interesting to note that *Cornuspira planorbis* was growing well in the presence of a different flora.) These same organisms are also the dominant flora in our circulating aquarium. Only three bacteria are common to all cultures. Eight species of small pennate diatoms and three species of blue-green algae comprise the common algal flora. These algae and bacteria are capable of supporting the growth and reproduction of large numbers of many species of foraminifera, under various laboratory conditions. Experiments in which this flora and *Streblus beccarii* were introduced into flasks of ASP_7, D, Erdschreiber and autoclaved sea water were successful. Cultures were incubated at 25 FC and fresh media were added weekly. During a six-month test period, growth and reproduction was most vigorous in the sea-water cultures. The foraminifera were found in an almost solid mass at the bottom of the flask (text-fig. 1). About one-tenth of this amount of growth was obtained in the artificial sea-water-based cultures. Additional experiments along these lines are in progress.

Dunaliella cultures have been observed to stimulate rapid pseudopod formation in starved cultures of *Globorotalia*, *Orbulina*, and *Quinqueloculina*. Even more interesting is the attraction of *Dunaliella parva* to certain species of foraminifera. If a specimen of *Streblus* is placed in a culture containing *Dunaliella parva*, a large percentage of the flagellate population will change from random locomotion and swim toward the specimen and its pseudopodal net. When they reach the test, or at times a short distance from the foram, they cease their locomotion and eventually lyse. The lysed cellular debris as well as other organisms become attached to the exterior cytoplasm of the foraminifera. Further investigations are in progress to determine the nature and extent of this phenomenon.

The results we have obtained with synxenic cultures of *Dunaliella parva* and several species of foraminifera under a variety of cultural conditions (different natural and artificial marine media enriched with natural and defined substrates) make it difficult to interpret the significance of the attraction mechanism in foraminiferal nutrition.



TEXT-FIGURE 2

Budlike organisms from an axenic culture of *Streblus beccarii* in sea water plus 10% horse serum.

Enrichment cultures

We have tried to stimulate the growth and reproduction of *Streblus beccarii*, *Trochammina* spp., and *Miliammina fusca* with a number of metabolites in axenic culture, synxenic culture with *Nitzschia acicularis* and *Dunaliella* spp., and agnotobiotic cultures. We have thus far tested the effects of a number of salts, metals, vitamins, sugars, amino acids, and natural materials such as egg albumin, herring DNA, yeast RNA, liver extract, casein hydrolysate, Trypticase, mixtures of fatty acids, horse serum, mud extracts and tomato juice. Some of these organic enrichments are apparently stimulatory; more defined experiments are in progress. The effect of horse serum is dramatic. Thousands of small budlike bodies (text-fig. 2) were obtained in axenic cultures of *Streblus beccarii* to which 1–10% horse serum was added. We have not had the opportunity to follow their formation in individual specimens.

DISCUSSION

The underlying causes affecting the distribution of foraminifera may be more complex than correlation of the usual ecologic factors lead us to believe. Very little is known about the subtle interplay between the foraminifera, their physio-chemical environment, and their inter-relationships with other microflora and fauna. While collecting littoral foraminifera, we have found areas where foraminifera are abundant, yet only a few feet away they are relatively scarce. Temperature, salinity, turbidity, pH, depth, and available light seem the same when measured in the field. On the basis of field studies alone it is very difficult to identify the critical factors limiting foraminiferal growth. While it is not possible to reproduce the complex elements of a natural environment in the laboratory, it is possible to study the basic physiological abilities of the foraminifera. From such studies, we may deduce the factors that may produce limiting conditions in a particular environment.

TABLE 1

ARTIFICIAL SEA WATER MEDIA WHICH SUPPORT THE GROWTH OF FORAMINIFERA

	ASP_7***	F_1	D**
NaCl	2.5%	2.7%	1.8%
$CaCl_2$	0.03%	0.05%	0.01%
KCl	0.07%	0.07%	0.06%
$NaNO_3$	0.005%	0.01%	0.05%
$MgSO_4 \cdot 7\ H_2O$	0.9%	0.9%	0.5%
Na_2 Glycerol Phosphate	0.002%	0.005%	—
$Na_2SiO_3 \cdot 9\ H_2O$	0.007%	0.003%	0.02%
P II metals*	3 ml/100	1 ml/100	3 ml/100
N T A	0.007%	0.003%	—
Vitamin mixture S_3**	1 ml/100	—	—
Vitamin mixture 8**	—	0.1 ml/100	—
$NaHCO_3$	—	0.005%	—
B_{12}	0.1 μg%	—	—
T R I S	0.1 %	0.05%	0.1%
K_2HPO_4	—	—	0.003%
Fe (electrolytically pure)	—	—	0.01 mg%

pH adjusted to 7.8–8.0 with NaOH

* See McLaughlin and Zahl 1959

** See Provasoli *et al* 1957 (similar to DC but without organic carbon sources)

*** Pintner and Provasoli 1958

The circulating aquarium in our laboratory has proven to be invaluable for the growth of foraminifera collected in small numbers from natural environments. Several species of *Bolivina*, *Planulina*, *Discorbis*, *Quinqueloculina*, *Pyrgo*, and *Elphidium* are flourishing in our aquarium in spite of the fact that small numbers were introduced. *Cornuspira planorbis* does not grow in our aquarium, although it was introduced several times and grows well in finger bowl culture. The different microflora observed in reproducing *Cornuspira* cultures may explain its exclusion from our aquarium.

Evaluation of algal organisms as potential food for foraminifera is not an easy task. The method of obtaining axenic foraminifera results in a loss of about 20% of the specimens during the serial transfers, because they cling to the inside of Pasteur pipettes, or are occasionally crushed. The difficulty and the time required to measure foraminifera limits experiments to small numbers (15–30 organisms). One hundred percent recovery of organisms from cultures is not usual. This, plus the initial loss in obtaining axenic specimens, leads to such a large experimental error that we chose to evaluate the majority of our experiments on the basis of reproduction or non-reproduction. Judging the success of monoxenic cultures on the basis of reproduction alone

allowed more time for the testing of potential food organisms, but eliminated the possibility of observing graded growth responses similar to those obtained by Davis and Guillard (1958) in their evaluation of microorganisms as foods for oyster and clam larvae.

It was interesting to note that neither the microorganisms they found most useful, (*Monochrysis lutheri, Isochysis galbana,* and *Dunaliella euchlora)* nor those found by Provasoli *et al.*, (1959) *(Rhodomonas lens* and *Isochrysis galbana)* supported the reproduction of synxenic cultures of foraminifera. When we further limit the algae in our multi-membered reproducing cultures, we may find it expedient to evaluate our results by measuring the organisms.

The relationship of *Dunaliella parva* (brine *chlamydomonas*) to foraminifera is of great interest. Both Grell (1954) and Bradshaw (1955) have found this a good food organism for *Rotaliella heterocaryotica*. Bělař, (1923, 1924) in his studies of *Actinophrys sol*, mentions that large numbers of green flagellates were immobilized in the vicinity of its pseudopods (as if a paralyzing secretion were produced by them) and thus formed a store of food to be ingested later. The similarity of our observations, regarding the attraction of *Dunaliella* to certain species of foraminifera, suggests that this might be a general phenomenon for food-gathering.

Of the many artificial sea water media tested, D, ASP_7, DMO and F_1, best support growth of foraminifera in agnotobiotic culture. Even though the populations of foraminifera in artificial media are usually not as large as in Erdschreiber or sea water, potentially the artificial media offer a more valuable starting point for the elaboration of the nutritional requirements of foraminifera. Sea water is inconstant in total inorganic ions, and in amount and kinds of dissolved and suspended materials. These variables prohibit definitive nutritional studies, even if done in axenic cultures. With the artificial media we now have we can test the effects of organic enrichments, major inorganic ions and trace elements on the growth and reproduction of axenically cultured animals. The success of this type of experiment permits the possibility of developing a completely synthetic environment in which all variables can be tested for their effect on the growth of many foraminiferal species.

Artificial media also have the advantage of offering greater critical control over potential food in synxenic cultures. Changing the constituents of the media (i.e., vitamins, NO_3^-, $PO_4^=$, or dissolved organic materials) will increase or suppress the growth of the food organisms.

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We wish to thank Drs. S. H. Hutner and L. Provasoli for their continued guidance and advice. The algae were from the culture collection at Haskins Laboratory. The original axenic isolations were made by Drs. L. Provasoli, J. C. Lewin, M. R. Droop, or J. J. A. McLaughlin. Dr. Allan Bé has provided us with living foraminifera from Bermuda. During the progress of this investigation the following people have rendered technical assistance which is gratefully acknowledged: Hans Behm, Jules Raynor, Katherine Moraci, Richard Honig, Jon Parets, Norman Block, and Michael Goldstein.

This work was started in 1950 by Angelina R. Messina and Brooks F. Ellis, when the first laboratory for the study of living foraminifera was established and the first living forms were brought back from Bimini, B.W.I. At that stage, and for many years thereafter, this work was financed entirely from departmental funds. In 1956 a grant was received from the Carter Oil Company to study the microforaminifera, and in 1959 a National Science Foundation grant, No. 10743, was received to study the basic biology of the foraminifera. Dr. McLaughlin is aided by National Science Foundation grant No. 9562.

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ABSTRACT

Many Uvigerinidae are important zone fossils in deep-water massive sandstones and mudstones of upper Oligocene and Miocene age in Raukumara Peninsula. Twenty-nine species and six subspecies are described, of which nineteen species and three subspecies are new. Subspecific classification is revised, five new genera and four new subgenera being established, partly on morphology and partly on lineage sequences. Time ranges are given in terms of eleven local zones which are correlated approximately with New Zealand stages and with European stages.

Upper Oligocene and Miocene uvigerinid foraminifera from Raukumara Peninsula, New Zealand

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INTRODUCTION

This paper is published by permission of Todd Brothers Limited, Wellington, New Zealand. Access to collections at the New Zealand Geological Survey were provided by Mr. N. de B. Hornibrook.

The foraminifera were collected from 1956 to 1958 by geologists of the Todd Brothers Oil Exploration Division from a lease area in Raukumara Peninsula, extending from 50 to 100 miles north of Gisborne and from the coast to about 20 miles inland. The northern part of the area includes the Waiapu and Poroporo valleys; the southern part includes Tokomaru Bay and the Ihungia and middle Mata valleys.

The area contains the type localities of the once well known but now disused Ihungia and Tutamoe "Series" (Ongley and MacPherson, 1928). These are not time divisions but correspond to the transitional (massive mudstone) and redeposited (graded bedded) facies of Wellman (1959).

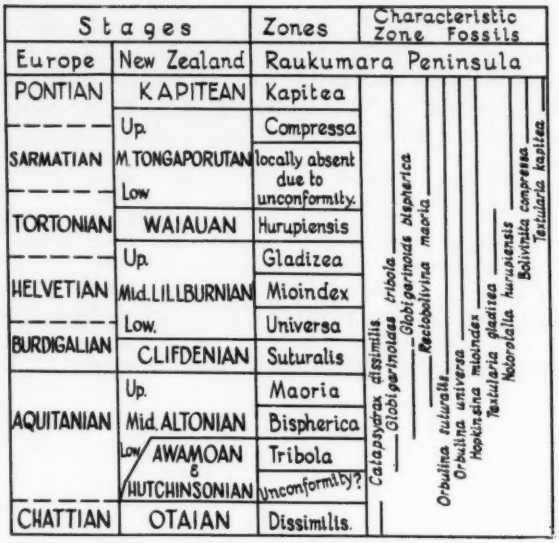
The upper Oligocene to middle Miocene is represented by 7,000 feet of massive calcareous mudstone in the Waiapu Valley, and about 15,000 feet of graded, bedded alternating sandstones and mudstones in Tokomaru district. The upper Miocene consists of massive mudstones and non-graded alternating sandstones and siltstones (Moore, personal commication) passing into massive shelf sandstone, and ranges in thickness from 200 feet in the west to more than 1,200 feet in the east.

Macrofossils are moderately common near the base of the shelf sandstone. They are extremely rare in the underlying massive mudstone facies. Occasional bands of transported molluscs occur in the graded bedded facies. Foraminifera are abundant in the massive mudstone facies and in the upper Miocene non-graded alternating facies, few in species and individuals in much of the graded bedded facies, and absent, probably owing to weathering, from most of the shelf sandstone. Micropaleontological zones are the only satisfactory detailed mapping units in the upper Oligocene to middle Miocene.

The massive mudstones contain a uniform, somewhat restricted range of benthic foraminifera and abundant individuals of many species of pelagic foraminifera. They contain extremely few Rotaliidae, Discorbiidae, Miliolidae, Elphidiidae, and other groups of foraminifera predominantly restricted to shallow water. Ostracodes, like mollusks, are extremely rare and Bryozoa are absent. The restricted benthic fauna indicates deposition in deep water, beyond the shelf, probably in the lower bathyal depth zone. The sea-floor was uniform, and most benthic species occur persistently within their stratigraphic ranges. Benthic species of restricted stratigraphic range are almost as reliable as pelagic species for zone correlation.

"Zone" is used in the sense recommended by Arkell (1933) for "belts of strata, each of which is characterized by an assemblage of organic remains of which one abundant and characteristic form is chosen as an index" (Marr, 1898). Each zone is named after its most useful guide fossil, the specific name alone being used, with a capital initial letter and not in italics (cf. Mariae Zone, Arkell, 1933).

The zones proposed below are intended to have local application only. Accurate correlation with the New Zealand stages is not possible now but may be possible



TEXT-FIGURE 1

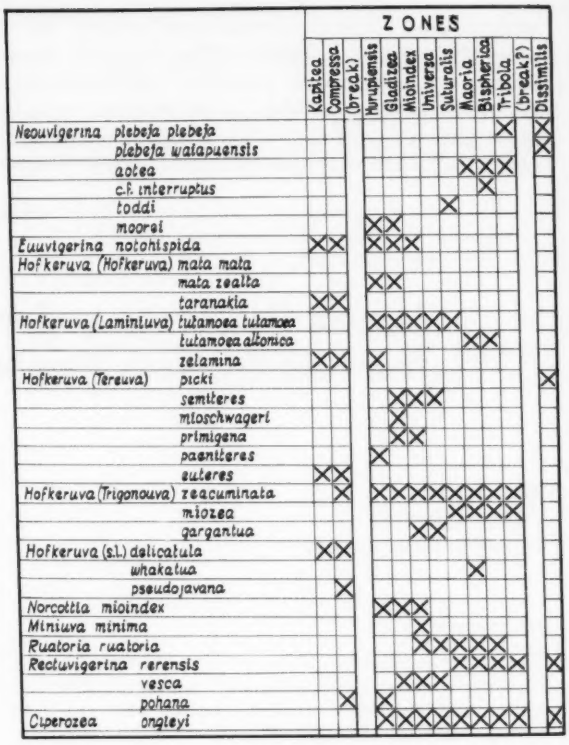
Correlation of northern Raukumara Peninsula foraminiferal zones with New Zealand and European stages. Characteristic zone fossils and their stratigraphic ranges shown on right. European stage correlations those of Hornibrook (1958, table I) slightly modified.

when foraminiferal zones have been defined at the type localities of the stages. Approximate correlation with New Zealand and European stages is shown in text-figure 1.

The zone ranges of the 32 species and subspecies of Uvigerinidae described are shown in text-figure 2. Species of *Angulogerina* are omitted because this group is being revised by Mr. N. de B. Hornibrook (in press).

CLASSIFICATION

Because their shell characters are few and variable, foraminifera are one of the most difficult animal groups to classify. The have been studied mainly by oil company micropaleontologists using them as a stratigraphic tool, and content to classify them merely as recognisable shapes. Within the last decade the taxonomy of two major groups, the "rotaliform" and the pelagic foraminifera, has been greatly refined by attention to details of shell structure once thought to be of minor significance. Taxonomy of the remainder of the smaller foraminifera has been neglected, except for Hofker's contributions, based on study of internal shell features. A few genera, such as *Haeuslerella* and *Ehrenbergina*, seem truly phylogenetic, but most are acknowledged as being merely form genera. Many are inconveniently large groups; the less bizarre the shape the greater is the number of species per "genus." The writer (1957) used morphology to subdivide certain miliolid "genera" into groups of related species. Probably *Textularia*, *Bulimina*, *Bolivina* and other "genera" could be treated similarly.



TEXT-FIGURE 2

Stratigraphic ranges of Uvigerinidae in Raukumara Peninsula, in terms of zones given in text-figure 1.

A few groups are difficult to subdivide solely on morphologic grounds, and one of these is the uvigerinid group with entirely triserial tests.

The main morphological features available for classifying triserial uvigerinids are size, overall shape, sculpture, and internal structures termed tooth-plates by Hofker (1951).

Tooth-plates are perhaps least subject to variation and hence the most reliable taxonomic guides, but they distinguish only three major groups apart from *Angulogerina*. Hofker's "genera" based solely on tooth-plates are groups of about sub-family rank. In most fossil specimens the tooth-plates are difficult to expose; consequently, a classification based on tooth-plates is impracticable. Fortunately there is a fairly consistent relationship between tooth-plates, sculpture and size. External morphology, used with discretion, distinguishes the tooth-plate groups, and is far more convenient in practice.

Sculpture is of three main types: 1) Costate – having longitudinal ribs. 2) Spinose – entirely covered with scattered, relatively large knobs or spines. 3) Hispid – partly or entirely covered with scattered fine papillae.

Contrary to current opinion, sculpture is particularly useful for defining uvigerine genera. The idea that sculpture is variable and has little taxonomic value is an attitude common in students of foraminifera and results from habits of thought handed down from early systematics. Variability, particularly variability of sculpture, is a bogey which has inhibited advance in taxonomy of many phyla (cf. the discussion of spiriferid brachiopods by Allan, 1947). No species of Uvigerinidae vary greatly in all characters. A few species vary considerably in one character, an extreme example being "*Uvigerina*" *peregrina* Cushman which varies from costate to spino-costate according to its environment. In contrast, the well-defined large genera *Rectuvigerina* and *Siphogenerina* both have consistent sculpture. The well-defined uvigerinid lineages in New Zealand have equally consistent sculpture.

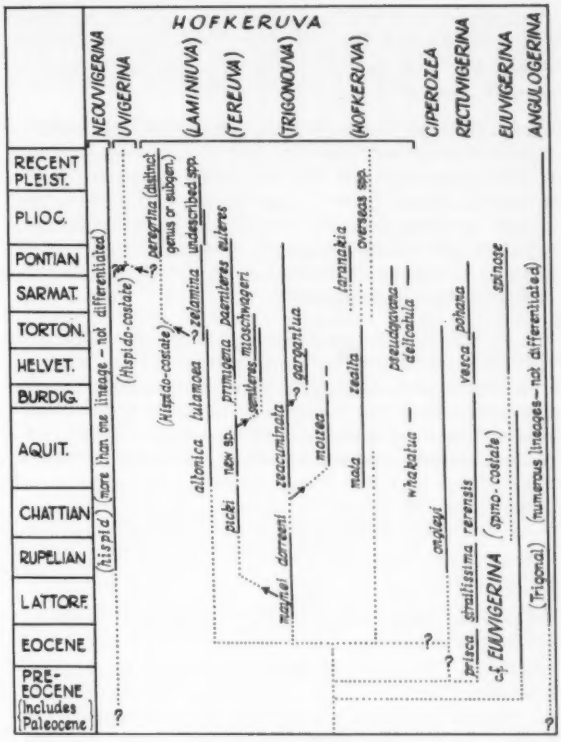
Size is useful, though less consistent than sculpture. Hispid forms are generally small. Spinose and most costate forms are relatively large. Some of the costate lineages described below are remarkably consistent in size.

In areas where rocks were deposited continuously, fossil foraminifera occur in continuous time sequences. They provide lineages which are the surest indicators of evolutionary relationship, because they show progressive changes from species to species.

Advances in classifying pelagic and "rotaliform" foraminifera have not rid modern foraminiferal taxonomy of the "form genus" tradition. Micropaleontologists persist in retaining the generic name *Globigerinoides* for intermediate members of the best established of all lineages, *Globigerinoides triloba* to *Orbulina universa*. Bolli (1957) referred a member of this lineage (*glomerosa* Blow) to the Eocene genus *Porticulasphaera*. Taxonomy should reflect evolution and should take into account sequence of forms in time. Similarity of shape does not always indicate phylogenetic relationship, homeomorphy probably being more common in foraminifera than in higher animal groups. Conversely, difference of shape, as shown by the ancestral lineage of *Orbulina*, does not disprove phylogenetic relationship. Emphasis should be directed to ancestry.

Classification of ammonites, in which stratigraphic position and morphology are considered together, is the best example of the evolutionary approach to taxonomy. Foraminiferal sequences are more certain than those of ammonites and classification of foraminifera by evolution is correspondingly easier.

Established lineages help to confirm or disprove the validity of species, and to show the time range of variation of species. Usually they display some consistent distinctive morphological feature or features. Lineages must not be neglected in any attempt to classify a group, and particularly a large group like "*Uvigerina*" which is difficult to subdivide on morphology alone. Where possible, lineages and groups of related lineages should be the main basis of paleontologists' subgenera and genera, as they are in large groups of Mollusca and other phyla.



TEXT-FIGURE 3

Inferred phylogeny of main groups of Uvigerinidae. Solid lines denote occurrences within New Zealand. Genera and subgenera shown in upper case italics, subgenera in brackets; species shown in lower case italics; New Zealand species of some genera only are shown.

FAMILY UVIGERINIDAE

The Uvigerinidae are a compact natural group. The siphonate aperture with phialine lip marks them off from the related Buliminidae and from most other calcareous foraminifera.

The form genus *Uvigerina* d'Orbigny was subdivided by Hofker (1951) into three genera, *Aluvigerina*, *Neouvigerina* and *Euuvigerina*, for which Thalmann (1952) subsequently designated *Uvigerina pigmea* d'Orbigny, *U. ampulacea* Brady and *U. aculeata* d'Orbigny respectively, as type species.

Uvigerina, a senior synonym of *Aluvigerina* (*fide* Ellis and Messina, Catalogue of Foraminifera), includes only a small group of Recent and late Tertiary species, and is not known in New Zealand. *Neouvigerina* comprises a large Tertiary and Recent group of finely hispid to smooth species of small to moderate size. Hofker's *Euuvigerina* contains a costate group of numerous species and a spinose group of relatively few species which includes the type species *E. aculeata*. For the costate

generations, and tend to become uniserial at the adult stage. A compact Tertiary group with these characters group the new generic name *Hofkeruva* is proposed, with *H. mata*, n. sp., as type species.

The inferred phylogeny of major groups of Uvigerinidae, together with the New Zealand Tertiary species, are shown in text-figure 3. *Hofkeruva* is the dominant genus in New Zealand. Four lineage groups of *Hofkeruva* are named as subgenera. The unnamed *peregrina* lineage, which has typical tooth-plates, but non-typical (spinocostate) ornament, must eventually be separated as a distinct subgenus or genus.

Species that link genera are not known in New Zealand and phylogenetic relationships (text-fig. 3) are inferred from similarities. *Hofkeruva*, *Ciperozea*, *Rectuvigerina* and *Euuvigerina* have the same type of tooth-plate. *Rectuvigerina* almost certainly evolved from a pre-Eocene *Hofkeruva* as it has consistent costate ornament. *Ciperozea* might have diverged from primitive *Rectuvigerina* or directly from *Hofkeruva*. *Euuvigerina* probably developed from *Hofkeruva* through the Eocene to Oligocene spinocostate group represented in New Zealand by *bortotara* and its allies.

Angulogerina and *Neouvigerina* differ from the hofkeruvid group in average size, forms of tooth-plates, shape and ornament. Each group contains several lineages of probable generic or subgeneric rank. The ancestry of the hispido-costate *Uvigerina* may be, as suggested by Hofker, in the Neouvigerinae, which have somewhat similar tooth-plates, or alternatively in the hispido-costate *peregrina* group.

SYSTEMATIC DESCRIPTIONS

Holotypes of new species described below are deposited in the New Zealand Geological Survey, unless stated otherwise. Paratypes of all except rare species are deposited in the United States National Museum, the National Museum of Victoria in Australia, and the Geology Department of Victoria University of Wellington in New Zealand.

LOCALITY NUMBERS

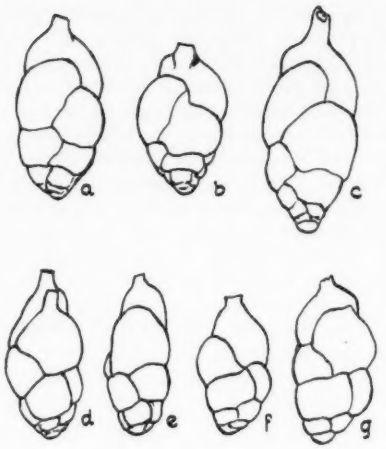
Where possible localities are referred to by the fossil record numbers in universal use in New Zealand, based on the national one-mile map sheet districts.

A few F numbers refer to localities of holotypes of previously described species, and are Geological Survey micropaleontological sample numbers.

Genus Neouvigerina Thalmann, 1952

Type species, by subsequent designation (Thalmann, 1952) *Neouvigerina ampullacea* (Brady) = *Uvigerina ampullacea* Brady, 1884.

The species *ampullacea* (Brady), *interrupta* (Brady), and *porrecta* (Brady) included in this genus by Hofker are relatively small, have only hispid ornament in all generations, and tend to become uniserial at the adult stage. A compact Tertiary group with these characters is clearly separate from the generally larger costate, hispido-costate and spinose uvigerine forms. Some of the forms can be traced more or less continuously through the upper Tertiary to the Recent. Tooth-plates of the New Zealand species could not be examined because the test are infilled with sediment, calcite or marcasite. *Neouvigerina* is a convenient group name for the hispid forms (*aculeata*, *hispida*, *rustica* and *notohispida* are spinose forms and are excluded). Several lineages are represented, but as they have not been closely studied further subdivision of the group is not attempted here. Some of the species appear to be widespread and to have long Tertiary ranges.



TEXT-FIGURE 4

a, b, c, *Neouvigerina plebeja waiapuensis*, n. sp., n. subsp. a, holotype, b, paratype. N. 72 f. 1562, c, paratype. N.72 f. 1571, × 110. d, e, f, g, *Neouvigerina, plebeja*, n. sp., paratypes N. 80 f. 764, × 110.

Neouvigerina plebeja Vella, new species
Plate 2, figure 19, text-figure 4d–g

Test very small, elongate, fusiform, solid; apex rounded; sutures moderately impressed, giving regularly lobulate outline; chambers inflated, slightly broader than high, increasing regularly in size, and coiled regularly so that sutures on successive whorls are usually in line, giving a characteristic neat appearance; sculpture, a few papillae, usually on the apex only; remainder of shell smooth and matt; apertural neck narrow, thin, often broken off.

Dimensions: Holotype 0.36 × 0.14 mm.

Age: Dissimilis to? Universa zones (Otaian to Lower Lillburnian, Chattian to Helvetian).

Locality of holotype: N.80 f. 764, 1¼ miles up Makara Stream, Mata Survey District, 4 miles 70 chs. at 282 degrees from Trig. 186 (Triloba zone).

Variation: Some specimens referred to this species are broader and generally about 30 percent larger than the type and may represent a different species. Papillae vary slightly in size and extent. Megalospheric and microspheric forms were not distinguished.

Remarks: Nondescript small shells of this type, common in New Zealand post-Eocene rocks have generally been classed as *Uvigerina* cf. *canariensis* d'Orbigny. *N. plebeja* is rare in the Oligocene (Dissimilis zone), common in the lower Miocene.

Neouvigerina plebeja Vella waiapuensis Vella, new subspecies
Text-figure 4a–c

Test small, solid, broad, with acuminate conical apex; sutures more deeply impressed between later chambers which become progressively more inflated and lobulate; maximum width usually above the middle; papillae largest and most numerous at the apex, but extending over most of the test.

Dimensions: Holotype 0.43 × 0.21 mm.

Age: Dissimilis zone (Otaian, Chattian).

Locality of holotype: N.72. f. 1562, east bank Waiapu River two miles north-east of Ruatoria township.

Remarks: A few specimens of *N. plebeja plebeja* occur with *N. plebeja waiapuensis* in some Dissimilis zone faunas. The two forms seem not to intergrade and possibly represent distinct species.

Neouvigerina aotea Vella, new species
Plate 2, figure 20

Test small, rather thin, elongate, subcylindrical, with bluntly rounded apex and depressed chambers; sutures impressed; early chambers ornamented with numerous scattered papillae; later chambers with papillae tending to become aligned longitudinally, usually coalescing to form continuous, fine, somewhat irregular ribs on adult chambers, reaching to the base of the neck on the terminal chamber; apertural neck short with a thin phialine lip.

Dimension: Holotype 0.51 × 0.23 mm.

Age: Triloba to Maoria zones (Altonian, Aquitanian).

Locality of holotype: N.80 f. 1429, Mata River, between Ihungia Road and Waikopiro Stream.

Variation: Shape is constant. Size varies about 20 percent; the development of costae is extremely variable, some specimens having only scattered papillae on all chambers, and some, like the holotype, having costae on all except the earliest chambers. Costae are never present on the initial quarter of the test.

Remarks: Pliocene and Recent hispido-costate groups such as *Uvigerina s.s.* and *Hofkerwa peregrina* have costae on the juvenile which become dissected into spines on the adult, and are larger than *N. aotea*. Ontogeny suggests that *N. aotea* had a hispid ancestor and its costae are secondary. *N. aotea* superficially resembles the New Zealand lower Tertiary spino-costate *bortotara*-group, but is more like *Neouvigerina* in its small, neat, compact shell and fine papillae. It is probably a branch of the *N. plebeja* lineage.

N. aotea is a useful index species, being known only from the Altonian Stage. It is persistent and common in the massive mudstone facies of Waiapu, and has been found to the south in Wairarapa and Nelson districts.

Neouvigerina cf. interrupta (Brady)
Plate 2, figure 7

Test small, elongate tending to become uniserial; sculpture of numerous scattered, tiny, elevated, rounded papillae; apex narrowly rounded; apertural neck long.

Dimensions: Hypotype 0.55 × 0.20 mm.

Age: Bispherica zone (Mid-Altonian, Aquitanian).

Locality of hypotype: N.80 f. 1300, 2¼ miles up Ihungia Stream, 20 chains at 360 degrees from Trig. Wharekia 181, Tokomaru Survey District.

Remarks: Only one specimen was found. It is distinct from all other species in the lease area but agrees closely with Brady's (1884, pl. 75, figs. 12–14) illustrations of Recent *interrupta*.

Neouvigerina? toddi Vella, new species
Plate 2, figure 15

Test large for the genus, elongate, subcylindrical, solid; chambers numerous, slightly broader than high, subquadrate to irregular in shape; sutures deeply incised outline slightly lobulate; apex broadly rounded; surface matt; nearly smooth with a few scattered, small, low, rounded tubercles concentrated near the sutures; neck short with prominent phialine lip.

Dimensions: Holotype 0.68 × 0.27 mm., paratype 0.51 × 0.27 mm.

Age: Suturalis zone (Clifdenian, Burdigalian).

Locality of holotype and paratype: N.80 f. 1758, grid. ref. 561, 513, headwaters of Mangara Stream.

Remarks: Though based on only two specimens, this species is clearly distinct, in its large, nearly smooth, subcylindrical test. Inclusion in *Neouvigerina* is provisional.

Neouvigerina moorei Vella, **new species**
Plate 2, figure 17

Test of moderate size, fusiform, broadest slightly above the middle; sutures incised between adult slightly lobulate chambers, flush and obscured by callous on early chambers; apex acute with small glassy terminal spine; sculpture of scattered, distant, tiny, rounded tubercles, more numerous near the apex and close to the sutures; apertural neck not distinctly marked off from the terminal chamber, tapered, surmounted by a solid phialine lip.

Dimensions: Holotype 0.64×0.30 mm.

Age: Gladizea to Hurupiensis zones (Upper Lillburnian to Waiauan, Tortonian).

Locality of holotype: N.80 f. 738, grid. ref. 561513, headwaters of Mangarara Stream (Gladizea zone).

Variation: Megalospheric and microspheric forms were not distinguished. Size varies about 20 percent; shape is fairly consistent but the apical cone varies from moderately convex to regularly tapering. The apical spine is missing from many specimens, probably having been broken off. The calloused conical apex and the relatively large size are typical.

Remarks: Though known only from the middle Miocene in the lease area this species almost certainly ranges up into the upper Miocene elsewhere in New Zealand. The lower limit of its range has not been established definitely but is probably close to the base of the Gladizea zone.

N. moorei is similar to, possibly conspecific with, the form illustrated by Bermudez (1949, pl. 13, fig. 48) as *U. mantaensis* Cushman and Edwards, from the "middle and upper Oligocene" (the lower part of the range of *Orbulina;* Burdigalian or Helvetian) of the Dominican Republic, but appears to be distinct from the type of *U. mantaensis.*

The species is named after W. R. Moore, formerly geologist for Todd Brothers Ltd.

Genus **Euuvigerina** Thalmann, 1952

Type species by subsequent designation (Thalmann, 1952) *E. aculeata* (d'Orb.) = *Uvigerina aculeata* d'Orbigny, 1846.

Tooth-plates of "*Uvigerina*" *notohispida* are simple twisted ribbon-like calcareous structures, running along the longitudinal axis of the test, passing through the aperture of each chamber and attached to the inner side of the rim of each aperture. They match the tooth-plates of *Euuvigerina aculeata* as described by Hofker. The costate "a2 generation" of *E. aculeata* described by Hofker was not found in New Zealand Tertiary faunas containing *notohispida* and has not been described for *rustica* or *hispida.* Nevertheless, the large spines of these species are characteristic and distinguish them from all other species. They form a compact group, commencing with *notohispida* and *rustica* in the middle Miocene. The ancestral stock is probably the spino-costate group represented in New Zealand by the Eocene–Oligocene *bortotara* lineage which like *notohispida* has strikingly different megalospheric and microspheric forms. The *bortotara* lineage is provisionally classed in *Euuvigerina.*

It is not certain that the Tertiary group is phylogenetically related to *E. aculeata,* and it may need a new generic name. It would be unwise, however, to erect a new genus without further investigation of the Recent species.

Euuvigerina notohispida (Finlay)
Plate, 2, figures 16, 18

Hopkinsina notoshispida Finlay, 1939, Roy. Soc. New Zealand, Trans., vol. 69, no. 1, p. 105, pl. 12, figs. 10–11. – Finlay and Marwick, 1947, New Zealand Jour. Sci. Technol., sec. B, vol. 28, no. 4, p. 234.

Uvigerina notohispida (Finlay). – Finlay, 1947, Roy. Soc. New Zealand, Trans., vol. 76, no. 3, p. 341. – Hornibrook, 1958, Micropaleontology, vol. 4, no. 1, p. 32.

The spines on later chambers are mostly low flat-topped cones; a few may be irregular in shape, but most are circular. On early chambers the spines are reduced in height with tops rounded, apparently by secondary deposits of shell on top of and between them. They are irregularly scattered with interspaces varying in width on individuals and from one individual to another, but generally not exceeding the width of the spines. The apertural neck is cylindrical, smooth and thin, frequently broken off.

Microspheric forms taper to an acute apex while the megalospheric forms are subcylindrical with a broadly rounded apex due to a very large proloculum. Microspheric forms tend to be slightly larger than the megalospheric.

Dimensions: Megalospheric hypotype 0.84×0.43 mm.; microspheric hypotype 0.91×0.43 mm.

Age: Mioindex zone to Kapitea zone (Middle Lillburnian to Kapitean, Helvetian to Pontian).

Localities of types: Holotype, F.3141, Kaiti Beach, Gisborne (Tongaporutuan, Sarmatian); hypotypes, N.72 f. 1259, grid. ref. 715393, Paoruku Stream, 1½ miles east of Waiapu River (Hurupiensis zone).

Remarks: E. notohispida is a useful stratigraphic index species at the top and bottom of its range, throughout New Zealand, but in the lease area its value is reduced because it is relatively rare.

Genus **Hofkeruva** Vella, **new genus**

Type species: Hofkeruva mata, n. sp.

Because of the similarity of tooth-plates Hofker grouped a costate form which he identified as *tenuistriata* (Reuss)

with *Euuvigerina aculeata*. Costate and spinose groups have been distinct since the latter appeared (as *E. rustica* and *E. notohispida*) in the middle Miocene. The partly uniserial costate genus *Rectuvigerina* has the same kind of tooth-plates and is phylogenetically closer to the costate group, having clearly developed from an unknown pre-Eocene costate uvigerinoid form. Costate uvigerinoid species first appear in the lower Oligocene in New Zealand. These and species of *Rectuvigerina* do not intergrade with the spino-costate "*Euuvigerina*" *bortotara* group.

The hispido-costate *peregrina* group, which appeared in New Zealand in the Pliocene, has entirely costate juveniles, suggesting a costate ancestor. The evolution of hispid ornament from costate ornament is a rare event, not common as has been inferred by students of foraminifera. Furthermore, in the hispid form of *peregrina* the costate character is not entirely lost because the papillae are never scattered at random but are aligned longitudinally. It may be desirable later to separate the *peregrina* group as a distinct genus, but provisionally it is classed in *Hofkeruva, sensu lato*.

Uvigerina pigmea though mainly costate is clearly distinguished from *Hofkeruva* by its tooth-plates. *Uvigerina* is a small group, probably confined to the Recent, and taxonomically isolated.

Costate species are the dominant Uvigerinidae of the Oligocene to Pliocene of New Zealand and apparently of most other parts of the world. The many lineages represented must eventually be grouped into several genera. Meanwhile, as a compromise, the entire group is separated as the genus *Hofkeruva* and four lineages are recognised as subgenera in New Zealand.

Though many tests were opened or sectioned, owing to infillings few tooth-plates could be examined. Tooth-plates of *Hofkeruva (Hofkeruva) mata* and *taranakia*, *Hofkeruva (Tereuva) picki* and *paenitere*s, *Hofkeruva (Trigonouva) mioschwageri* and *Hofkeruva (Laminiuva) tutamoea* were found to be identical with those of *Euuvigerina aculeata* and *Hofkeruva* "*tenuistriata*" as described by Hofker (loc. cit.), i.e., simple, transversely curved, twisted, ribbon-like plates passing through the apertural necks and joined to the top interior of each apertural neck.

The type species, *H. mata*, is an elongate form, similar and almost certainly related to *H. tenuistriata* (Reuss). The type figure of *tenuistriata* is poor and diverse forms have been described under the name of *tenuistriata*. This species therefore is not suitable to be nominated as type species.

Subgenus Hofkeruva Vella, new subgenus

Elongate tests of moderate size with ornament of narrow axial ribs, typically extending to the base of the apertural neck; compactly coiled and neat.

The subgenus is represented in New Zealand by the Miocene lineage *mata – zealta – taranakia*.

Hofkeruva (Hofkeruva) mata Vella, new species
Plate 2, figures 3–4

Test small, elongate, elliptical, rather solid, with moderately impressed sutures; adult chambers slightly undercut in some specimens; outline somewhat lobulate; sculpture, numerous narrow, crisp, steeply bevelled, sharp-crested ribs, narrower than interspaces, usually stopped at the sutures, less commonly continous from one chamber to the next; ribs on initial chamber commencing with tiny spinose projections on a few specimens, but usually not spinose, increasing in height gradually from the apex to the sides of the terminal chamber, then tapering rapidly, generally extending to the base of the neck, but on a few fully grown tests not reaching the neck; apertural neck rather narrow, short, with thin phialine lip; apex bluntly acuminate not differing perceptibly in microspheric and megalospheric individuals.

Dimensions: Holotype 0.54 × 0.24 mm., paratype 0.51 × 0.26 mm.

Age: Triloba to Suturalis zones (Altonian to Clifdenian, Aquitanian – Burdigalian) grading up to the middle Miocene chronological subspecies *zealta*.

Variation: Tests do not approach the uniserial condition as do specimens illustrated under the name of *Uvigerina tenuistriata* by Cushman (1918, pl. 22, fig. 7) and by Dieci (1959, pl. 6, figs. 8–9, as varieties *gaudryinoides* Fornasini and *siphogenerinoides* Fornasini). Size varies about 50 percent.

Remarks: H. mata is similar to the form figured as *U. bifurcata* d'Orbigny from the lower Miocene of Sumatra by Leroy (1944, pl. 5, fig. 28).

H. mata is rare in the massive siltstone facies but abounds in partly graded bedded sediments with a few transported Mollusca on the western side of the Tutamoe Syncline (Ongley and MacPherson, 1928). It is probably a transported shallow-water species.

Hofkeruva (Hofkeruva) mata Vella zealta Vella, new subspecies
Plate 2, figure 2

Test more solid than typical *mata* with thicker ribs, less lobulate outline, and usually more acute apex.

Dimensions: Holotype 0.53 × 0.26 mm.

Age: Universa to Hurupiensis zones (Lower Lillburnian to Waiauan, Helvetian to Tortonian).

Locality of holotype: N.80 f. 738, Mata River 1¼ miles downstream from Waikopino Stream junction, Tutamoe Survey District, 50 chains at 075 degrees from Trig. 177A.

Variation: Size, shape and strength of ribs are fairly constant.

Remarks: H. mata and *zealta* form a temporal cline, grading apparently continuously from one form to the other. An arbitrary boundary is taken at the base of the Universa zone.

Hofkeruva (Hofkeruva) taranakia Vella, new species
Plate 2, figure 1

Test small, solid, elongate usually tapered to bluntly acuminate apex; sutures slightly impressed, hardly interrupting the outline; ribs few, widely spaced, strongly raised thick flanges, most of them continuous from the apex to the terminal chamber, usually reaching to the base of the neck; apertural neck short, broad, with thin phialine lip.

Dimensions: Holotype 0.63 × 0.33 mm.

Age: Compressa to Kapitea zones (Upper Tongaporutuan to Kapitean, Pontian).

Locality of holotype: N.81 f. 643, grid ref. 373512, Te Puia, Compressa Zone.

Variation: Shape varies a good deal. Many specimens are ovate rather than regularly tapered, and irregularities in growth are common. The sculpture is the most consistent feature.

Remarks: The marked difference in sculpture suggests that this is probably not a lineal descendant of *H. mata zealta*. Because of an unconformity in the lease area, it is not known whether or not the two forms intergrade.

Subgenus Laminiuva Vella, new subgenus

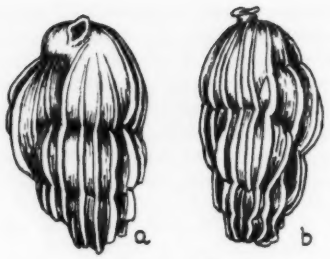
Type species: Hofkeruva (Laminiuva) tutamoea Vella, n. sp.

Test of moderate to large size, with numerous thin, elevated, flange-like axial ribs, usually continuous from apex to terminal chamber, typically reaching the base of and even encroaching on the neck; profile irregular owing to deeply impressed sutures and inflated chambers.

Laminiuva is proposed for a New Zealand Miocene to Pliocene lineage. No comparable overseas species are known and this subgenus is probably endemic. The lineage appears as a small form, close to the type species, in the Bispherica zone of the lease area and in the lower Altonian or Awamoan of east Wellington. The antecedents of this small species are not known. The type species *tutamoea* ranges from the Suturalis to the Hurupiensis zone, and is replaced by *zelamina* in the Compressa and Kapitea zones. *Laminiuva zelamina* is known in the upper Miocene of east Wellington where it is in turn replaced by an undescribed species in the lower Pliocene.

Hofkeruva (Laminiuva) tutamoea Vella, new species
Plate 1, figure 4

Test of moderate size, widest near the middle, with irregularly lobulate outline and truncated apex; numerous flangelike ribs, thin and hyaline at their outer edges, irregularly serrated by breakage, produced to tiny spines at the apex; interspaces wider than the ribs; apertural neck short, broad, with thin upward-curving phialine lip.



TEXT-FIGURE 5

Hofkeruva (Laminiuva) tutamoea altonica, n. subsp. a, paratype, b, holotype, × 110.

Dimensions of holotype: 0.68 × 0.39 mm.

Age: Suturalis to Hurupiensis zones (Clifdenian to Waiauan, Burdigalian to Tortonian.

Locality of holotype: N. 80 f. 1426, Mata River, north of Waikopiro Stream junction (Gladizea zone).

Variation: Slight; size, lobulation and sculpture are consistent.

Hofkeruva (Laminiuva) tutamoea Vella altonica Vella, new subspecies
Text-figure 5a, b

Smaller than typical *tutamoea* with lower, thicker ribs.

Dimensions of holotype: 0.53 × 0.31 mm.

Age: Bispherica and Maoria zones (middle to upper Altonian, Aquitanian). In east Wellington, lower Altonian or Awamoan, lower Aquitanian.

Locality of holotype: N. 159 f. 592, grid ref. 570781, middle Tinui Valley, East Wellington (lower Altonian or Awamoan).

Repository: Geology Department, Victoria University of Wellington.

Remarks: This subspecies grades up to typical *tutamoea*. Maoria zone specimens are generally distinctly smaller than *tutamoea* but are sometimes difficult to separate.

Hofkeruva (Laminiuva) zelamina Vella, new species
Plate 1, figure 3

Test large, subcylindrical, gently tapering to bluntly rounded apex; impressed sutures obscured by sculpture of numerous heavy longitudinal flangelike ribs with crests not serrated by breakage, not indented at the sutures, continuous from apex to summit of terminal chamber, thicker than those of *tutamoea*, not produced to apical spines; aperture as in *tutamoea*.

Dimensions of holotype: 0.85 × 0.37 mm.

Age: Hurupiensis to Kapitea zones (Waiauan to Kapitean, Tortonian to Pontian).

Locality of holotype: N. 80 f. 1368, Mata River near Waikopiro Stream junction (Hurupiensis zone).

Variation: Size varies about 50 percent. Sculpture is consistent and the most diagnostic feature. Microspheric and megalospheric forms were not distinguished.

Subgenus **Tereuva** Vella, **new subgenus**

Type species: Hofkeruva (Tereuva) paeniteres (Finlay) = *Uvigerina paeniteres* Finlay, 1939.

Tests of moderate to large size with lobulate outline, apertural neck sunken in a shallow depression; sculpture of longitudinal ribs or flanges, generally continuous on successive chambers, strongest on early chambers, decreasing toward adult chambers, and always absent from the upper surface of the terminal chamber.

Tereuva is probably endemic to New Zealand. The earliest species which can be included definitely in the lineage is *Hofkeruva (Tereuva) picki*, n. sp., known from as early as the Waitakian stage (middle Oligocene) (Hornibrook, personal communication). The latest species is the almost completely smooth *Hofkeruva (Tereuva) euteres* of the Compressa and Kapitea Zones (Pontian). The group almost certainly developed in New Zealand from the lower Oligocene plexus of *Hofkeruva (Trigonouva) maynei* (Chapman), which includes varieties whose adult tests tend to become smooth. The group is not a linear evolutionary sequence but is distinguished by progressive retreat of the costae from the adult part of the test.

Hofkeruva (Tereuva) picki Vella, **new species**
Plate 1, figure 10

Test of moderate size, obese, solid, ovate to subcylindrical, with broadly rounded or obtusely angled apex, sutures impressed, chambers moderately inflated; sculpture of about 14 primary ribs with broad interspaces, strongly raised, sometimes produced to small spines at the apex, continuous over sutures, tapering towards the adult, obsolete by the penultimate chamber, very faint on the lower part of the terminal chamber, not reaching the upper surface; a few weak interstitial ribs on post-juvenile chambers; apertural neck short, broad with usually broken thin phialine lip, sunken in a shallow depression.

Dimensions of holotype: 0.85 × 0.45 mm.

Age: Dissimilis zone (Otaian, Chattian).

Locality of holotype: N. 72 f. 590, Poroporo River beside main highway (Dissimilis zone).

Variation: The ribs of the holotype coalesce at the apex, but in many specimens, possibly the microspheric form, they commence discretely and are produced to minute spines near the apex. The degree of smoothness of the terminal chamber is variable.

Remarks: This species does not occur in the shelf facies of the Otaian in the South Island and is assumed to be a deep water form. It is confined to the Dissimilis zone in the lease area, but has been identified by Hornibrook (personal communication) in the Waitakian Stage (Rupelian—Chattian) elsewhere in New Zealand.

Care is needed to distinguish *Tereuva picki* from two later forms – an undescribed Altonian (Aquitanian) species which has a more conical shape in the juvenile test, more acute apex, and less regular, often twisted sculpture; and the Lillburnian (Helvetian) *primigena*, which has consistently weaker sculpture.

Hofkeruva (Tereuva) semiteres Vella, **new species**
Plate 1, figures 13, 14

Test of moderate size, stout, solid, with deeply impressed sutures and irregular lobulate outline; sculpture of few irregular flangelike ribs, some dying out quickly on the juvenile part of the shell, some persisting on to the penultimate chamber; apex profile irregular owing to sudden termination of rib-flanges at different levels, more or less acuminate in the microspheric form, bluntly truncated in the megalospheric; apertural neck short, broad, situated in a shallow depression, and furnished with a thin phialine lip upturned at the rim. *Dimensions of holotype:* 0.89 × 0.45 mm.; paratype 0.86 × 0.46 mm.

Age: Universa to Gladizea zones (Lillburnian, Helvetian).

Locality of holotype and figured paratype: N. 80 f. 1406 Mata River, north of Waikopiro Stream junction (Universa or Mioindex zone).

Remarks: H. (Tereuva) semiteres is smaller than *mioschwageri* and has shorter, fewer rib-flanges and a less acuminate apex. No other species of *Tereuva* has similar flangelike ribs.

Hofkeruva (Tereuva) mioschwageri (Finlay)

Uvigerina mioschwageri FINLAY, 1939, Roy. Soc. New Zealand, Trans., vol. 69, pt. 1, p. 103.

Test large, sub-conic, widest near the adult end, with elongate acuminate early test; elevated flangelike ribs on the early shell, dying at about the penultimate chamber. Adult end of shell smooth; apertural neck short with flaring phialine lip.

Age: Gladizea zone (upper Lillburnian, upper Helvetian or Tortonian).

Locality of holotype: N. 97 f. 498, Waikura Stream, Poverty Bay.

Variation: The costae of *mioschwageri* are consistently flangelike. Generally they are continuous from one chamber to the next and somewhat twisted. In some specimens they are discrete on each chamber and not in line, forming irregularly disposed, flattened finlike projections.

Remarks: T. mioschwageri is rare in the lease area.

T. mioschwageri and *T. semiteres* seem to be closely related species and are considered to have diverged from the main line of *Tereuva*. The acuminate shape and twisted costae suggest that *mioschwageri* developed from the unnamed Altonian species (noted in text-fig. 3).

Hofkeruva (Tereuva) paeniteres (Finlay)

Uvigerina paeniteres FINLAY, 1939, Roy. Soc. New Zealand, Trans., vol. 69, pt. 1, p. 103.

Test large, with somewhat inflated chambers and lobulate outline; sculpture of obsolete axial ribs visible on juvenile chambers only.

Age: Hurupiensis zone (Waiauan, Tortonian).

Locality of holotype: F. 3132, Kaiti Beach, Poverty Bay (probably Waiauan).

Remarks: Tereuva paeniteres is preceded by an ancestral form with heavier sculpture in the Mioindex and Gladizea zones and followed by a virtually smooth descendant in the Compressa and Kapitea zones. The early form grades up to typical *paeniteres*. The hiatus between the Hurupiensis and Compressa zones in the lease area obviates grading from *paeniteres* to the smooth form there, but from scattered lower Tongaporutuan faunas elsewhere a gradational relationship appears to exist. The group appears to be a temporal cline, which evolved from moderately costate to smooth. Three chronospecies are recognised with arbitrary boundaries defined as follows:

Kapitea zone	... *euteres*
Compressa zone	... *euteres*
(Zones missing)	
Hurupiensis zone	... *paeniteres*
Gladizea zone	... *primigena*
Mioindex zone	... *primigena*

Hofkeruva (Tereuva) primigena Vella, new species
Plate 1, figure 12

Large, obese, widest above the middle, with rounded apex; sculpture distant low axial ribs, continuous from the apex, very weak on adult chambers, but most reaching the terminal chamber.

Dimensions of holotype: 1.0 × 0.57 mm.

Age: Mioindex and Gladizea zones (middle and upper Lillburnian, Helvetian—Tortonian).

Locality of holotype: N. 80 f. 1448, Mata River north of Waikopiro Stream junction.

Remarks: This species is most useful at its first appearance. It enters at about the same horizon as *Euuvigerina notohispida* and *Norcottia mioindex*, marking the base of the Mioindex zone.

Hofkeruva (Tereuva) euteres Vella, new species
Plate 1, figures 6–7

Test of moderate size with impressed sutures and lobulate outline, entirely smooth, or with faint traces of longitudinal ribs on the initial part of the shell only.

Dimensions of holotype: 0.75 × 0.38 mm., paratype 0.63 × 0.37 mm.

Age: Compressa and Kapitea zones (upper Tongaporutuan and Kapitean, Pontian).

Locality of holotype and figured paratype: N. 80 f. 705, near main highway, Tokomaru Survey District, 3 miles 5 chains at 265 degrees from Trig. K. 62, Compressa zone.

Variation: Shape varies from squat and globose to broadly elliptical.

Subgenus Trigonouva Vella, new subgenus

Type species: Hofkeruva (Trigonouva) zeacuminata, n. sp.

Tests of moderate to large size with moderate to strong axial costae; juvenile and usually also the adult roughly triangular in cross section.

Costate uvigerinoid tests of triangular habit seem to occur in the Miocene of many countries, but it is unlikely that all are phylogenetically closely related. In New Zealand *Trigonouva* appears first near the base of the Oligocene (Whaingaroan Stage) as *maynei* (Chapman), is followed in the middle Oligocene (Waitakian Stage) by *dorreeni* (Finlay), and in the upper Oligocene and Miocene (Pareora, Southland and Taranaki Series) by *zeacuminata*, n. sp. These three species probably constitute a direct lineage. *Trigonouva miozea* (Finlay) is considered to be a short-lived offshoot of the main lineage. The extraordinarily large species *gargantua* appears suddenly at the base of the Universa zone apparently without ancestors in New Zealand.

Hofkeruva (Trigonouva) zeacuminata Vella, new species
Plate 1, figures 15, 16

Test of moderate to large size, solid, broadest near the adult end, tapering with lightly convex profile, little indented by weakly impressed sutures, and acutely pointed not spinose apex; sculpture, moderately high, steeply bevelled, longitudinal ribs with narrowly rounded crests continuous from apex to adult chambers, some bifurcating, increasing in height from the apex to the first third, then diminishing gradually towards the adult end, usually dying on the terminal chamber shortly below the base of the neck; apertural neck variable in length, rather broad with thick phialine lip.

Dimensions of holotype: 0.86 × 0.44 mm.; paratype 0.82 × 0.46 mm.

Age: Triloba to Compressa, possibly Kapitea zones (lower Altonian to ?Kapitean, Aquitanian to Pontian).

Locality of holotype and figured paratype: N. 71 f. 1160, grid. ref. 689347, stream north of Willow Stream, Rotokautuku (Universa zone).

Variation: Size varies about 50 percent. Many specimens (megalospheric form?) have a slightly truncated apex with a few ribs produced to small spines.

Remarks: This species is readily distinguished by its trigonal early test, tapering form, usually acutely pointed apex, strong mostly continuous axial ribs and small smooth area at the summit of the terminal chamber. It is the commonest, most widely distributed species in the Miocene rocks of the lease area and occurs extensively in upper Oligocene and Miocene elsewhere in New Zealand.

Hofkeruva (Trigonouva) miozea (Finlay)
Plate 1, figures 5, 8–9; plate 2, figure 6

Uvigerina miozea FINLAY, 1939, Roy. Soc. New Zealand, Trans., vol. 69, pt. 1, p. 102, figs. 12–14.

Supposed microspheric and megalospheric forms require separate descriptions.

Microspheric: Ovate varying from stout to narrow, with moderately impressed sutures and slightly lobulate profile; subtrigonal in transverse section; apex narrowly rounded without spines at the ends of the ribs.

Megalospheric: Subcylindrical with truncate apex usually bearing spines formed by prolongation of the ends of ribs; sutures deeply impressed; profile very lobulate; trigonal shape obscure.

Common features: Test rather small, with short broad apertural neck and heavy phialine lip; sculpture of low broadly rounded longitudinal ribs not crossing sutures, heaviest on early chambers, becoming progressively finer on later chambers, finally becoming hair-thin.

Dimensions of hypotypes: Microspheric, 0.55 × 0.34 mm.; megalospheric, 0.61 × 0.40 mm. (pl. 1 fig. 8), 0.59 × 0.32 mm. (pl. 1 fig. 9).

Age: Triloba to Suturalis zones (lower Altonian to Clifdenian, Aquitanian to Burdigalian).

Localities of types: Holotype: F. 5389 North Bank, Mangaoporo River, Waiapu district (Suturalis zone); hypotypes: microspheric, N. 80 f. 1765, grid. ref. 555512, Kouetumarae Stream (Triloba zone), megalospheric N. 72 f. 520 Poroporo River, Waiapu district (Bispherica zone); N. 71 f. 645, Whakatu Stream, Waiapu district (Maoria zone).

Remarks: The name *miozea* has been applied loosely to several upper Miocene and Pliocene species. The range of variation is much less than has been supposed. Many Triloba and Bispherica zone populations have obsolescent sculpture. The illustrated megalospheric test (pl. 1 fig. 5) has very fine distant riblets even on the juvenile chambers and has no apical spines. It is possible that this early form is separable from *miozea s.s.*

The holotype of *miozea* is the form here described as microspheric. It is not firmly established that the form described as the megalospheric is not a distinct species. The two forms seem to have the same stratigraphic range, but they are not found together at all places, and their morphologic differences are greater than is usual between alternate generations of *Hofkeruva*.

Hofkeruva (Trigonouva) gargantua Vella, new species
Plate 1, figure 11

Test very large, solid, broadly conic, widest near the adult end, tapering to narrowly rounded apex; the three initial angles accentuated by heavy broadly rounded ribs; other ribs obscured by callous on early test, appearing on later chambers then diminishing to become obsolete by the final chamber; sutures slightly impressed on adult test, obscured by callous on juvenile test.

Dimensions of holotype: 1.07 × 0.60 mm.

Age: Universa to Mioindex zones (lower to middle Lillburnian, Helvetian).

Locality of holotype: N. 80 f. 719, Mangahoui Stream, Mata Survey District, 6 miles 10 chains at 262 degrees from. Trig. Puketite (Mioindex zone).

Variation: The three initial angles are sometimes less accentuated and the intervening ribs less obscured by callous than on the holotype.

Remarks: This species is conspicuous because of its size. It is rare but widespread in the massive mudstone facies. In some respects it resembles *zeacuminata* and may be a derivative of the local lineage. It appears suddenly at about the same horizon as *Orbulina universa*, without any known ancestors and is most likely and emigrant.

Hofkeruva, sensu lato

Three species of doubtful and unknown affinities are described under the generic name *Hofkeruva*, but are not allocated to a subgenus.

Hofkeruva delicatula Vella, new species
Plate 2, figure 5

Small, subcylindrical, with slightly inflated chambers and slightly undercut sutures; sculpture of crisp, narrowly rounded costae not continuous over sutures tending to form prickles at the base of each chamber, and prolonged to small spines at the truncate apex.

Dimensions of holotype: 0.41 × 0.25 mm.

Age: Compressa zone (upper Tongaporutuan, Sarmatian or Pontian).

Locality of holotype: N. 80 f. 1304, grid. ref. 590510, Mata Road, one mile east of Fernside Road junction.

Variation: Size, shape and ornament are quite constant in seven paratypes from the type locality. Prickles are not always present at the base of each chamber.

Remarks: This tiny, elegant species is not unlike lower Miocene tests referred to *Trigonouva miozea* and may be a derivative of that species. It is not transversely trigonal. A similar form has been seen in the Waiauan of Hawkes Bay.

Hofkeruva whakatua Vella, new species
Plate 2, figure 11

Shell of moderate size, broadly ovate, with lightly impressed sutures scarcely visible on the early part of the test; sculpture of few, widely spaced, strong flange-like ribs with thin outer edge serrated by breakage, generally extending from apex to just below the summit of the final chamber; apertural neck short, broad, with phialine lip thin and seldom preserved.

Dimensions of holotype: 0.73 × 0.50 mm.

Age: Maoria zone (upper Altonian, upper Aquitanian).

Locality of holotype: N. 71 f. 645, Whakatu Stream, Waiapu District.

Remarks: Known only from the type locality where 30 specimens were found.

Though it has ribs like those of *Laminiuva tutamoca*, *H. whakatua* is distinguished from all the *Laminiuva* group by its squat shape, the smooth upper surface of its terminal chamber, and the wide spacing of its ribs. It is probably related to the Javanese species figured as *Uvigerina crassicostata* Schwager by Boomgaart (1949, pl. 12, fig. 8).

Hofkeruva pseudojavana Vella, new species
Plate 1, figures 1–3

Test of moderate size, squat, broadly ovate, with lightly impressed sutures indistinct on the early part; megalospheric form with bluntly truncated apex, microspheric with an acute apex with a prominent spine; sculpture of strong narrowly rounded ribs continuous from apex to penultimate chamber or lower part of final chamber; greater part or all of terminal chamber smooth; apertural neck short, rather narrow; phialine lip not seen.

Dimensions of holotype (microspheric): 0.58 × 0.40 mm., figured paratype (megalospheric) 0.67 × 0.45 mm.

Age: Compressa zone (upper Tongaporutuan, Pontian).

Locality of holotype: N. 80 f. 1258, grid. ref. 547508, Pauariki Stream, Tokomaru District.

Remarks: H. pseudojavana is known only from the type locality, represented by 10 specimens.

It resembles *H. whakatua* but is easily distinguished by its smaller size, lower, more rounded ribs, smoother terminal chamber, and prominent apical spine on the microspheric form. The megalospheric test is similar to the form illustrated as *Uvigerina javana* Koch by Boomgaart (1949, pl. 12, fig. 10).

Genus Norcottia Vella, new genus

Type species: *Norcottia mioindex* (Finlay) = *Hopkinsina mioindex* Finlay, 1947.

Small, narrowly lanceolate, neat, with elevated chambers, strongly incised sutures; triserial throughout; ornament of close fine longitudinal costae made faintly gemmulate apparently by microscopic transverse riblets; apertural neck slender, well developed with a thin flaring phialine lip.

In placing *mioindex* in *Hopkinsina*, Finlay was evidently influenced by its elongate ovate shape and fine regular ornament. The type of *Hopkinsina* (the Louisiana Eocene *H. danvillensis* Howe and Wallace) has a triserial initial stage forming one-quarter to one-third of the test, followed by a slightly twisted but essentially biserial stage. The outline is nearly smooth, sutures being hardly impressed. The apertural neck is rudimentary and oval in shape. No related species are known in New Zealand. *Norcottia* has more in common with the uvigerinoid group than with *Hopkinsina*. Most specimens have an obscurely trigonal juvenile stage. Tooth-plates were not

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PLATE 1
All figures × 70

1, 2 *Hofkeruva pseudojavana* Vella, n.sp.
1, holotype, microspheric; 2, paratype, megalospheric.

3 *Hofkeruva (Laminiuva) zelamina* Vella, n. sp., holotype.

4 *Hofkeruva (Laminiuva) tutamoea* Vella, n. sp., holotype.

5, 8, 9 *Hofkeruva (Trigonouva) miozea* (Finlay)
5, megalospheric N.72 f. 520 Bispherica Zone; 8, 9, microspheric N. 80 f. 1765 Triloba Zone.

6, 7 *Hofkeruva (Tereuva) euteres* Vella, n. sp.
6, holotype; 7, paratype.

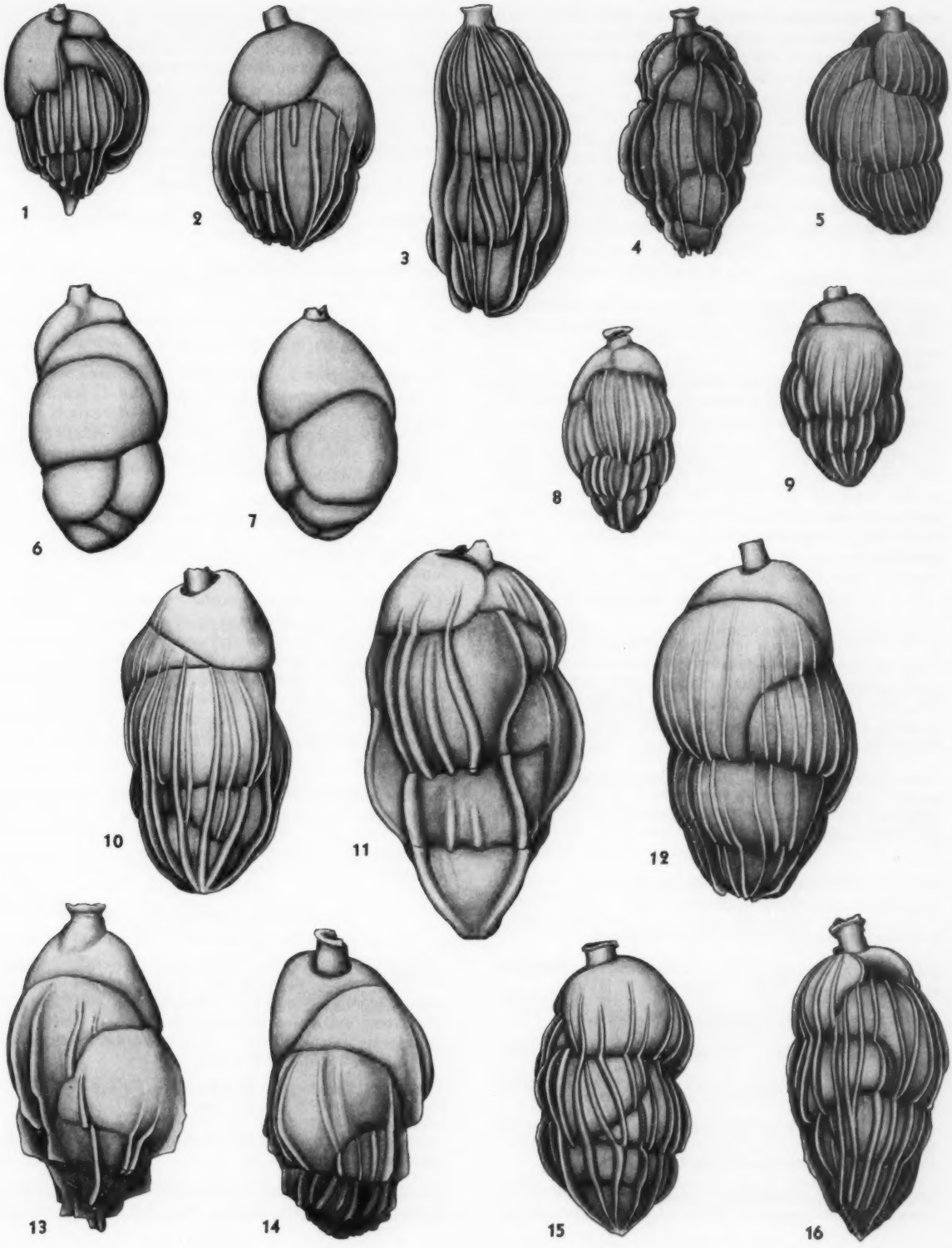
10 *Hofkeruva (Tereuva) picki* Vella, n. sp., holotype.

11 *Hofkeruva (Trigonouva) gargantua* Vella, n. sp., holotype.

12 *Hofkeruva (Tereuva) primigena* Vella, n. sp., holotype.

13, 14 *Hofkeruva (Tereuva) semiteres* Vella, n. sp.
13, holotype; 14, paratype.

15, 16 *Hofkeruva (Trigonouva) zeacuminata* Vella, n. sp.
15, paratype; 16, holotype.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seen, all specimens opened having been filled with matrix or secondary deposits, but the small size and regular placing of chambers suggest relationship to *Angulogerina*.

The species is taxonomically isolated.

Norcottia mioindex (Finlay)
Plate 2, figure 14

Hopkinsina mioindex FINLAY, 1947, New Zealand. Jour. Sci. Technol., sec. B, vol. 28, no. 5, pp. 282–283, pl. 5, figs. 80–82.

Dimensions of hypotype: 0.59 × 0.19 mm.

Age: Mioindex to Hurupiensis zones in the lease area, Lillburnian to Kapitean elsewhere (Helvetian to Tortonian).

Localities: Holotype, F. 5305, Porangahau Survey District, Hawkes Bay (Lillburnian?); hypotype, N 81, f. 609, Tokomaru Bay (Hurupiensis zone).

Remarks: N. mioindex is a fairly persistent species throughout New Zealand. It appears suddenly in abundance at the base of the Mioindex zone, and disappears suddenly, without descendants, at the top of the Kapitea zone. Being distinctive and abundant, it is an invaluable index fossil.

Genus **Miniuva** Vella, **new genus**

Type species: *Miniuva minima*, n. sp.

Tiny, triserial, tending to uniserial, moderately elongate, with somewhat irregular lobulate habit; sculpture of irregular longitudinal costae not continuous over sutures; apertural neck very short with slightly reflexed lip.

Like *Norcottia mioindex* this species is taxonomically isolated. Its aperture is distinctive. Its habit is too irregular for *Norcottia* and its minuteness excludes it from *Hofkeruva*.

Miniuva minima Vella, **new species**
Plate 2, figures 8–10

For description see generic diagnosis above.

Dimensions of holotype: 0.29 × 0.10 mm., figured paratypes 0.31 × 0.12, 0.25 × 0.09 mm.

Age: Mioindex zone (Lillburnian, Helvetian).

Locality: N. 72 f. 1349, Waiapu River, near Ruatoria.

Remarks: Known definitely only from the type locality.

Genus Ruatoria Vella, **new genus**

Type species: *Ruatoria ruatoria*, n. sp.

Small, narrow, elongate, initially triserial, last two or three chambers staggered uniserial, irregularly lobulate with deeply impressed sutures; sculpture narrow distant costae not continuous over sutures, not reaching the upper part of the final chamber; apertural neck broad, slightly constricted at the middle expanding to somewhat irregular flaring lip.

Ruatoria ruatoria Vella, **new species**
Plate 2, figures 12–13

For description see generic diagnosis.

Dimensions: Holotype 0.45 × 0.13 mm.; paratype 0.43 × 0.11 mm.

Age: Bispherica to Mioindex zones (mid-Altonian to mid-Lillburnian, Aquitanian to Helvetian).

Locality of holotype and figured paratype: N. 72 f. 1429, Bispherica zone, Waiapu River, near Ruatoria.

Remarks: No related New Zealand species are known but *Siphogenerina panggoensis* Leroy from the Telisa formation (Miocene) of Sumatra is similar. *Ruatoria* is easily distinguished from *Rectuvigerina* by its smaller size, irregular profile, staggered terminal chambers and rather distinctive aperture.

Genus **Rectuvigerina** Mathews, 1945

Type species: By original designation, *Siphogenerina multicostata* Cushman and Jarvis, 1929.

The New Zealand Oligocene to Miocene sequence *striatissima* (Stache)—*rerensis* (Finlay)—*vesca* (Finlay)—*pohana* (Finlay) shows progressive change from coarse-ribbed to fine-ribbed. The change is not gradual, successive species invading suddenly and replacing the pre-existing species. Being widespread and easy to recognize, they are superlatively useful index species. All are most common in the massive calcareous mudstone facies.

R. vesca is probably close to the Java Miocene species figured as *Siphogenerina striata* (Schwager) by Boomgaart (1949, pl. 9, fig. 2). Other New Zealand species are possibly related to contemporaneous overseas species.

Rectuvigerina rerensis (Finlay)
Plate 2, figures 22–23

Uvigerina tenuistriata Reuss. – CHAPMAN, 1926, New Zealand, Geol. Survey, Pal. Bull., no. 11, pl. 14, fig. 9.
Siphogenerina rerensis FINLAY, 1939, Roy. Soc. New Zealand, Trans., vol. 69, no. 1, p. 110, pl. 11, fig. 8.
Rectuvigerina rerensis (Finlay). – MATHEWS, 1945, Jour. Pal., vol. 19, no. 6, p. 596, pl. 82, fig. 15.

Dimensions of Hypotypes: N. 72 f. 1562, 0.82 × 0.22 mm., N. 72 f. 1245 0.72 × 0.22 mm.

Age: Dissimilis to Suturalis zones (Otaian to Clifdenian, Chattian to Burdigalian).

Localities of types.: Holotype, F.3029 Whangara Beach, Poverty Bay. Hypotypes N.72 f. 1562, Waiapu River,

Dissimilis Zone; N.72 f. 1245, grid. ref. 728393, Maramatoitoi Stream (Triloba Zone).

Remarks: Distinguishing characters are the relatively heavy, strongly raised, rather widely spaced costae, depressed chambers with flattened ribs and slightly incised sutures. The microspheric form has a single apical spine, the megalospheric has costae produced to form a number of smaller apical spines.

Rectuvigerina vesca (Finlay)
Plate 2, figures 24–25

Siphogenerina vesca FINLAY, 1939, Roy. Soc. New Zealand, Trans., vol. 69, no. 1, p. 109, pl. 13, figs. 46–47.
Rectuvigerina vesca (Finlay). – MATHEWS, 1945, Jour. Pal., vol. 19, no. 6, p. 598, pl. 81, fig. 7.

Dimensions of hypotypes: 0.85 × 0.19, 0.69 × 0.20 mm.

Age: Universa to Gladizea zones (lower to upper Lillburnian, Helvetian).

Localities: Holotype F.5105, Citrini's Area, near Kumara, Greymouth. hypotypes, N.71 f. 1160 grid. ref. 689347, Willow, near Rotokautuku (Universa Zone).

Remarks: R. vesca is distinguished from *rerensis* by its more slender, more delicate test, more elevated, subglobular adult chambers, and finer sculpture. The microspheric and megalospheric forms each have a single large apical spine.

Rectuvigerina pohana (Finlay)
Plate 2, figure 26

Siphogenerina pohana FINLAY, 1939, Roy. Soc. New Zealand, Trans., vol. 69, no. 1, pp. 109–110, pl. 13, figs. 44–45.
Rectuvigerina pohana (Finlay). – MATHEWS, 1945, Jour. Pal., vol. 19, no. 6, p. 395, pl. 82, figs. 10–11.

Dimensions of hypotype: 0.69 × 0.20 mm.

Age: Hurupiensis to Compressa, or Kapitea zones (Waiauan to upper Tongaporutuan or Kapitean, Tortonian to Pontian).

Localities: Holotype F.3099, Uawa Survey District, east of Trig. 166, Poverty Bay, Compressa Zone (upper Tongaporutuan, Sarmatian or Pontian).

Remarks: Smaller than *vesca*, with very fine close ribs. Found in great numbers, but in relatively few samples. In the Mata River, in Tutamoe district, hybrid populations of *Rectuvigerina pohana* × *vesca* and of *Plectofrondicularia pohana* Finlay × *parri* Finlay mark the base of the Hurupiensis Zone.

Genus Ciperozea Vella, new genus

Type species: *Ciperozea ongleyi* (Finlay) = *Siphogenerina ongleyi* Finlay, 1939 (upper Oligocene to Miocene, New Zealand).

In *Rectuvigerina* the adult chambers become rectilinear immediately above the triserial stage which is usually less than half the test; the longitudinal ribs are prominent and extend from suture to suture, a high proportion extending across the sutures from one chamber to the next. In contrast *Siphogenerina ongleyi* has a large triserial portion, does not become truly rectilinear, and has ornament of low ribs tending to become very finely prickly in well preserved specimens, dying on the upper surface of the terminal chamber, and stopped abruptly and neatly in line, slightly above the suture at the base of each chamber.

The New Zealand lower Eocene species *S. prisca* Finlay is similar but smaller and may be an early member of the group.

Siphogenerina seriata Cushman and Jarvis closely resembles *ongleyi*. Specimens in the New Zealand Geological Survey collection, No. 12 from the Cipero Marl of Trinidad, have finer ribs tending to become obsolete, with more pronounced prickliness, but stopped in the same way, neatly in line at the base of each chamber. Another similar form occurs in the Suva Soapstone, having very fine obsolete ribs on later chambers, an apical spine and a number of small spines at the beginnings of ribs on the initial chambers.

The relatively weak ribs stopped above the sutures to give the chambers an undercut appearance, the large triserial stage and staggered uniserial adult chambers distinguish the group from *Siphogenerina* and *Rectuvigerina*.

Ciperozoa ongleyi (Finlay)
Plate 2, figure 21

Siphogenerina ongleyi FINLAY, 1939, Roy. Soc. New Zealand, Trans., vol. 69, no. 1, p. 111, pl. 13, figs. 42–43.
Rectuvigerina ongleyi (Finlay). – MATHEWS, 1945, Jour. Pal., vol. 19, no. 6, p. 594, pl. 81, fig. 18.

Dimensions of hypotype: 0.80 × 0.37 mm.

Age: Dissimilis to Hurupiensis zones (Otaian to Waiauan, Chattian to Tortonian). First appears in Waitakian (Rupelian) elsewhere in New Zealand.

Localities: Holotype, F.5093 Porangahau – Wimbledon Road, Hawkes Bay (Waitakian, Rupelian). Hypotype, N. 72 f. 1565, Waiapu River (Dissimilis Zone).

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PLATE 2
All figures × 70

1 *Hofkeruva (Hofkeruva) taranakia* Vella, n. sp., holotype.

2 *Hofkeruva (Hofkeruva) mata zealta* Vella, n. subsp., holotype.

3–4 *Hofkeruva (Hofkeruva) mata* Vella, n. sp., holotype.

5 *Hofkeruva delicatula* Vella, n. sp., holotype.

6 *Hofkeruva (Hofkeruva)* cf. *miozea* (Finlay)
N.71, f.645 (Maoria Zone).

7 *Neouvigerina* cf. *interrupta* (Brady)
N.80, f.1300 (Bispherica Zone).

8–10 *Miniwa minima* Vella, n. sp.
9, holotype; 8, 10, paratypes.

11 *Hofkeruva whakatua* Vella, n. sp., holotype.

12–13 *Ruatoria ruatoria* Vella, n. sp.
12, holotype; 13, paratype.

14 *Norcottia mioindex* (Finlay)
N.81, f.609, Hurupiensis Zone.

15 *Neouvigerina toddi* Vella, n. sp., holotype.

16, 18 *Euuvigerina notohispida* (Finlay).
16, microspheric; 18, megalospheric N. 72, f.1259 (Hurupiensis Zone).

17 *Neouvigerina moorei* Vella, n. sp., holotype.

19 *Neouvigerina plebeja* Vella, n. sp., holotype.

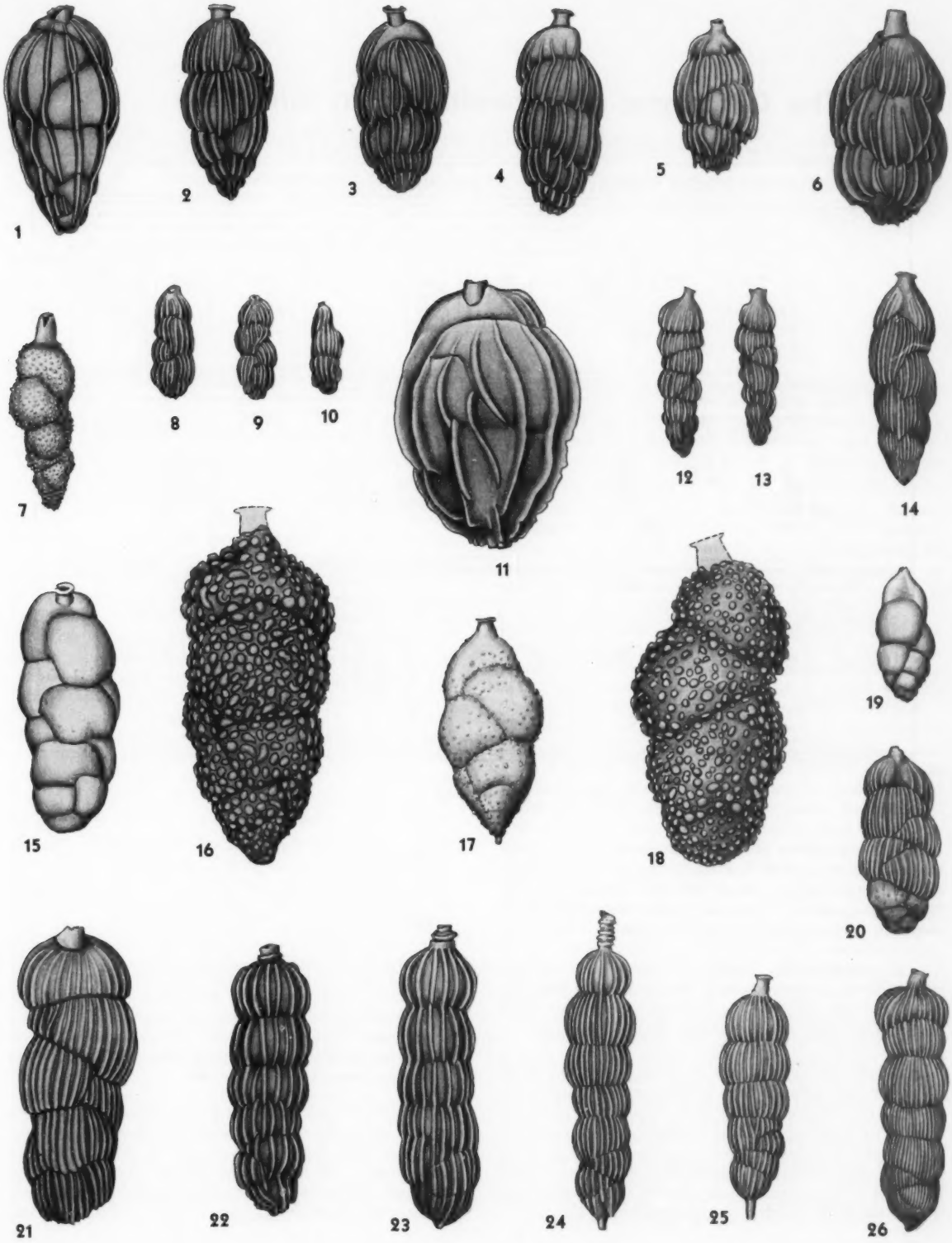
20 *Neouvigerina aotea* Vella, n. sp., holotype.

21 *Ciperozea ongleyi* (Finlay)
N.72, f.1565 (Dissimilis Zone).

22–23 *Rectuvigerina rerensis* (Finlay)
22, megalospheric N. 72, f. 1245 (Triloba Zone); 23, microspheric N. 72, f. 1562 (Dissimilis Zone).

24–25 *Rectuvigerina vesca* (Finlay)
N. 71, f. 1160 (Universa Zone); 24, microspheric; 25, megalospheric.

26 *Rectuvigerina pohana* Finlay
N. 81, f. 617. (Compressa Zone).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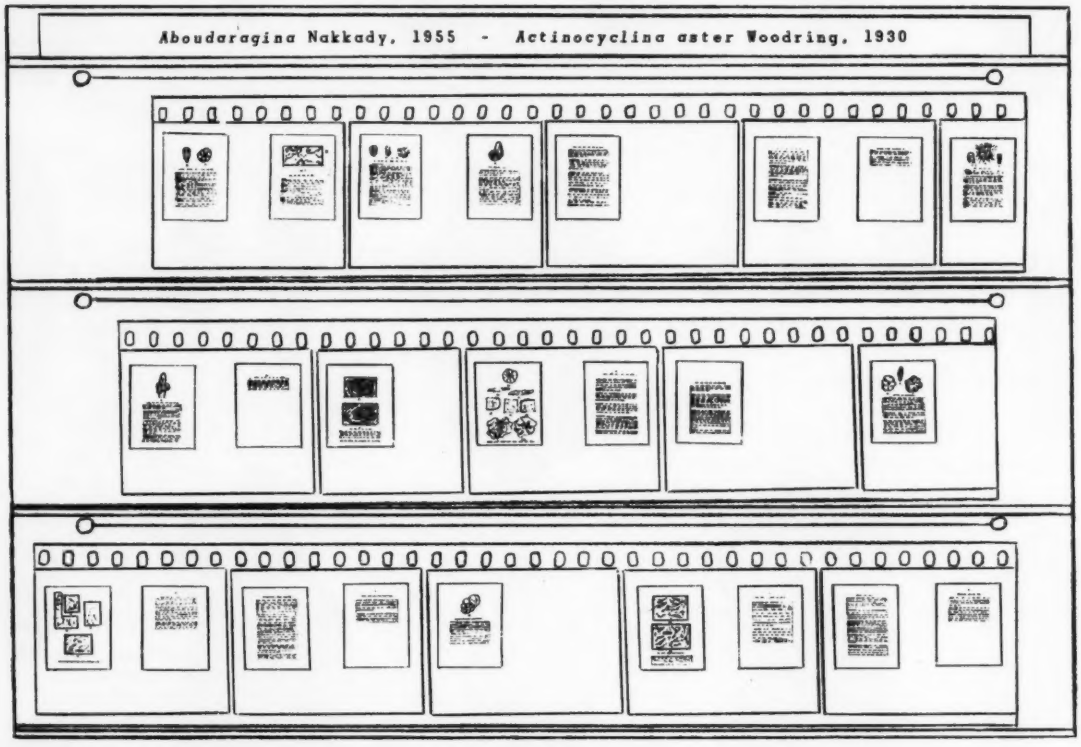
The Catalogue of Foraminifera in microfilm



TEXT-FIGURE 1

The printed edition of the Catalogue of Foraminifera was exhausted in 1958. A new printing cannot be undertaken because of the great cost. The demand for the Catalogue continues, however, and a microfilm edition has been prepared to meet this demand.

The microfilm edition consists of thirty-three 100 foot rolls of 35 mm. film on which the Catalogue, complete through 1958, has been reproduced. More than 1580 genera and 25,275 species are included in this edition.

The rolls of film can be used as issued or cut into strips of four or five frames each and filed in transparent plastic holders (text-figure 1) supplied with each microfilm copy of the Catalogue. These holders can accommodate a total of fifteen frames each, and each frame can be viewed individually in a special flat-bed viewer. Space in which to file supplementary frames can be provided by not filling the holders to capacity initially.

Supplements to the microfilm edition are issued annually and consist of a roll of 35 mm. film. If the transparent holders are being used for the original copy, the supplements should be cut into individual frames and interfiled in the proper places to maintain the alphabetic arrangement. The supplementary frames can be interspliced in the original rolls if a conventional type reader is to be used.

The Catalogue, filed in the transparent holders, can be accommodated in four 5 × 8 × 24 inch file drawers. Self-adhering labelling strips are also supplied with the plastic holders.

This microfilm edition of the Catalogue of Foraminifera is now available on a subscribing membership basis. Inquiries and applications should be directed to the Department of Micropaleontology, The American Museum of Natural History, Central Park West at 79th Street, New York, N. Y. THE EDITORS.

Effect of the 1959 International Botanical Congress on nomenclature of fossil spores and pollen

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NOMENCLATURE VS. CLASSIFICATION AND TAXONOMY

Much that has been written and said about fossil pollen and spore nomenclature in recent years has been the result of attempts to achieve a unified nomenclatural "system" for pollen and spores. This is understandable as a direct result of the spectacular increase in numbers of kinds of fossil spores that have been described. Seeing the creation of many obvious synonyms and the use of long lists of names that seem awkward or undesirable, some palynologists have tended to confuse two aspects of systematic paleobotany, i.e., nomenclature and classification. By nomenclature, in this instance, is meant the application of permanent, formal names to plants represented by fossil spores and pollen. As spores and pollen are fossil plant organs, and represent taxa of plants, the application of such names falls under the jurisdiction of the International Code of Botanical Nomenclature (Lanjouw, 1956), which provides an approved procedure for naming all kinds of modern and fossil plants, including those represented by isolated fossil pollen, spores, and other types of microfossils worthy of naming. The rules concerning *organ* genera and species, and *form* genera and species, apply equally to fossil pollen and other fragmental fossil specimens showing diagnostic structures. The nomenclature so provided is basically binomial, as are all formal animal and plant names in scientific usage. The technique of application of binomial nomenclature is relatively stable, since the International Code approaches universal acceptance. It is based on the more or less rigid application of the dual principles of priority and the type method. The methods of nomenclature are distressingly legalistic to some persons, but they do provide a standard and well understood means of reference. A taxon of given circumscription, position, and rank can have only one correct name. Binomial nomenclature has now been in use for 200 years, and the present International Code is the result of two centuries of experience of thousands of biologists and paleontologists. It is the one botanical nomenclatural code that is subject to periodic orderly review at the International Botanical Congresses, held every four or five years, in peacetime. All this is not intended to mean that every specimen of fossil pollen and spores must be given a binomial label. Symbols, code designations, and the like always can, and often should be, used instead. But when formal nomenclature is used, the names should be in accordance with the International Code.

Classification is different from nomenclature. Classification is the arrangement of entities into systems, either for convenience, or to illustrate principles of relationship. If constructed only for convenience of use, such systems are likely to be highly artificial. If items in the system are grouped in order to show phylogenetic relationship (or imagined relationship), the system is, to some extent, "natural". All natural or phylogenetic classifications so far devised are partly artificial, because, even among the best known modern plants, some details of ancestry are far from clear. Classification of plants (taxonomy), in contrast to plant nomenclature, is not subject to any international control and should not be. Ideas of relationship change as knowledge increases. Techniques for placing items within a system (identification) improve, by introduction of entirely new concepts of anatomical interpretation, by new methods of dealing more precisely with data, and by new technical methods of study. Changes of this nature will be rejected or accepted by the scientific public on the basis of their usefulness in practice and soundness in theory. Modification in systems of classification will continue as long as scientific work continues, but practice in use of formal nomenclature is not affected *per se* by any new scheme of classification.

There is a temptation to confuse the concept of a group in classification, and the name the group happens to bear. Or, as has happened in paleopalynology, it may even be suggested that a system of classification be used for the manufacture of names of forms not yet discovered (cf. van der Hammen, 1956). Perhaps it is forgivable to restate the point that formal nomenclature isn't even necessary to classification. Tschudy (1957), for example, has published a classification of pollen types without names — a classification, pure and simple, using symbolic designation for the units.

TABLE 1

A COMPARISON OF FORMAL NOMENCLATURE WITH INFORMAL ARTIFICIAL CLASSIFICATION OF FOSSIL PLANTS

	Formal paleobotanical nomenclature	Systems of informally recognized paleobotanical classification
Governed by	Formal provisions of the International Code of Botanical Nomenclature.	Usage and scientific concensus. No international conventions apply.
Purpose	Provide stable nomenclature; names not subject to change, except for formally recognized reasons and in rigidly prescribed ways.	1. Provide classificatory systems for identification of fossils. 2. Provide means of indicating presumed natural relationships of fossil groups.
Validity of names and priority	Validity determined by priority only, providing names are properly established in accordance with provisions of Code. A relatively few exceptions, clearly specified in the Code are recognized: *nomina conservanda*.	Validity not established by convention. Systems are accepted or rejected according to preference of individual paleobotanists. Priority usually recognized but not binding.
Kinds of names used and technique of naming	Latin or latinized words, per provisions of Code.	Numbers, letters, symbols, or informal technical words preferable to distinguish clearly the categories indicated from taxa with valid Latin names.
Typification and illustration	Every taxon must have its nomenclatural type, to which the name is permanently affixed, either as a synonym or as a name in correct usage. Illustration is required for validation of a new specific or infraspecific taxon, post 1912; rank of a new taxon must be designated, post 1953.	At liberty of author, but in order to avoid confusion with formal nomenclature, types should not be designated. Examples can be cited to aid in identification.
Technique of publication	Name and description must be published per the provisions of the Code, otherwise names are invalid, or illegitimate, according to the case.	At liberty of author.
Examples of units	Names of taxa: *Engelhardtia triletipollenites* Rouse; *Parasporites maccabei* Schopf; *Illinites elegans* Kosanke.	Designations of divisions: CP_2 (Tschudy, 1957) Psila XXX (van der Hammen, 1956 – although he called this a "sub-genus") Trichotomosulcites (Erdtman, 1947).

Table 1 is an attempt to demonstrate graphically the salient points of difference between informal classification and formal nomenclature, as they apply to paleobotany.

There has been considerable discussion of desirable practices in the creation of names for fossil pollen. Wodehouse (1933) and, more recently, Rouse (1957) proposed techniques for coining microfossil names so as to show, by the names themselves, the taxonomic position of the fossils. *Hymenophyllumsporites* Rouse, for example, would be a spore genus related to the extant fern genus *Hymenophyllum*. Others have also proposed series of names that attempt direct morphological description of the fossils by the names themselves. An example is *Intratriporopollenites* Pflug and Thomson. Such names are valid and legitimate if requirements of the Code are met, but binomial nomenclature has developed as a means of avoiding the necessity of imparting description by the name itself. Names such as those proposed by Thomson and Pflug are inconvenient and unwieldy. The description attempted is inadequate anyway, and fails its purpose. Binomial nomenclature developed precisely in opposition to long descriptive polynomials that were used by pre-Linnaean botanists, and to some extent by Linnaeus himself (cf. Stearn, 1959). The present botanical code is pointed in stating that names are intended only for easy reference to a taxon, not to describe it. Adequate description of the taxon is to be sought elsewhere.

THE "MESS" IN PALYNOLOGICAL NOMENCLATURE

What then of the alleged mess in palynological nomenclature? To use Rouse's words (1957, p. 349–350): "To date, there has been no general or international agreement concerning the nomenclature of plant microfossils, and the variations existing in systems of different schools have resulted in a confusing array of names and classifications. This unfortunate situation

is progressively compounded with each additional publication." Kremp (1959) has inquired "Can expanding palynology escape taxonomic chaos?" Other authors have expressed similar doubts. Neophytes find this situation distressing and are confused about the distinction between nomenclature and classification.

Systematic treatment of plant microfossils presents difficulties for various reasons, of which perhaps the most disturbing are that (1) they are normally found dispersed from the plant organs in which they were borne, and that (2) they are known from studies of modern plants to have widely varying degrees of distinctiveness. In response to the perceived difficulties, various systems of classification have been proposed which have unfortunately attempted to provide formal nomenclature for taxa, along with the classification. The confusion to which Rouse, Kremp, and others refer is of two kinds. One source of confusion is that the systems of classification of various authors overlap and conflict. As shown in Table 1, this is not a matter for concern. In fact, it is a good thing, for systems of classification evolve by experimentation, use, and selection. This should have nothing to do with nomenclature. Whether one selects as the correct name for a taxon *Porocolpopollenites orbis* Pflug and Thomson depends not on whether he accepts and follows Pflug's "system" but on whether *P. orbis* is the earliest validly published legitimate name for the taxon one is considering.

The second sort of confusion to which Rouse refers is truly nomenclatural, and results from the publication of synonyms or additional names for taxa that have already been named. Regarding synonymy, nomenclature in paleopalynology is in as good condition as nomenclature in biology and paleontology in general. To be sure, there are lists of synonymy in plant micropaleontology. But in works on neobotanical taxonomy one finds no shorter, in fact much longer, lists of synonyms. Nor are all synonyms the result of mistakes. Any taxon that has been much studied will accumulate a synonymy as a result of variation in taxonomic concepts. The solution of the problem is careful monographic study by specialists on the various groups, not imposition of nomenclatural systems by fiat. If names for fossil pollen were uniformly coined according to some anagrammatic scheme, the real problems of synonymy and homonymy would be in no wise helped. Neobotanists found out long ago that priority and the application of the type method of nomenclature yield the most reasonable result in the long run.

Zoölogists have tended more than botanists toward creation of commissions to rule by fiat on nomenclatural questions, with the result that the officially ordained rulings on, and exceptions to, the zoölogical code have become a sizable body of nomenclatural law in several volumes. But the zoölogists have not yielded to the expediency of creating official "systems" of nomenclature with prescribed combinations of syllables having specific meanings. Despite the same temptations to which palynologists are subject, the zoölogists have relied basically on priority and typification as the most reasonable cornerstones of nomenclature. They have rejected, as redundant, proposals to create formal artificial systems of nomenclature-classification for entities, so-called parataxa, of uncertain affinity or fragmental preservation.

As to the assertion that there has been no international agreement on paleopalynological nomenclature, it should be noted that there has been widespread agreement that names applied to taxa based on fossil pollen and spores are governed by the International Code of Botanical Nomenclature, just as are taxa based on other kinds of plant fossils. The 1954 Code itself (Article 7, p. 15) states, for example: "...The typification of... genera based on plant microfossils (pollen, spores, etc.) ...does not differ from that indicated above." A slightly revised wording of this statement was approved at the 1959 botanical congress which removes any possible doubt on this matter.

PREPARATION FOR THE NOMENCLATURAL SESSIONS, NINTH INTERNATIONAL BOTANICAL CONGRESS

Paleobotanists in general, and palynologists in particular, explored the various faults and alleged faults of paleobotanical nomenclature more thoroughly in the period between the Paris 1954 Eighth International Botanical Congress and the Montreal 1959 Ninth International Botanical Congress than during any similar period, at least as measured by the number of published papers and formal proposals. To *Taxon*, by now known to most paleobotanists, must go much of the credit. Paleobotanists, including paleopalynologists, submitted about fifty formal proposals to amend the Code. These, and related considerations, were rather thoroughly discussed in *Taxon* and elsewhere in print. In addition, there were numerous papers presented at scientific sessions, for example at the well-attended roundtable discussions of systematic microfossil paleobotany sponsored by the Paleobotanical Section, Botanical Society of America, in East Lansing, Michigan, in 1955, and Storrs, Connecticut, in 1956. It is not an exaggeration to state that at no time has the paleobotanical public had such a complete airing of views on this subject, with the result that the Committee for Paleobotanical Nomenclature of the Bureau of Nomenclature that met at Montreal in August, 1959, probably was better instructed and prepared than any of its predecessors. The committee had before it proposals ranging from the relatively extreme one of van der Hammen, proposing what amounted to a separate code for paleopalynology, to conservative ones aimed at eliminating contradictions and inadvertent mistakes in the Paris 1954 Code (also called the 1956 Code because of publication date). As a result of the action of this committee, the status of paleobotanical nomenclature within the framework of the International Code seems to this writer better now than it ever has been.

It might be well to record the observation that the Section of Nomenclature at the international botanical congresses takes a "hands off" attitude toward matters of paleobotanical nomenclature, leaving them almost entirely to the paleobotanical committee for decision. Thus, paleobotanists have only themselves to blame for the condition of the Code, if they fail to submit formal proposals to the Congress and analytical articles to *Taxon*, as well as attend and take part in the nomenclatural sessions of the Congress.

RESULTS OF THE 1959 CONGRESS AFFECTING NOMENCLATURE

The results of the nomenclatural sessions at Montreal, affecting paleopalynology (as a part of paleobotany), are summarized in Table 2. In brief:

1) The most significant change was the acceptance of a proposal by A. T. Cross to abolish the erstwhile paleobotanical appendix, as such, and incorporate its provisions in the main body of the Code. The change was adopted as a result of much thought and discussion before and during the Congress. The separate appendix was objectionable both conceptually and practically. There was an implication that the appendix outlined provisions for paleobotanical nomenclature much more completely than it did, and paleobotanists were inclined to overlook the main rules that were modified by provisions in the appendix. Much better organization is achieved by having the paleobotanical provisions printed together with the rules they affect. The existence of the appendix also had the very unfortunate effect of directly causing editorial errors. There were a number of instances of this in previous versions of the Code. For example, in the Paris 1954 Code (Lanjouw, 1956) Article 32 used the words "recent plants" in describing the requirements of effective publication and description, thereby effectually excluding fossil plants from this important provision of the Code. This glaring mistake, now corrected, was a product of the right hand not knowing what the left hand was doing. With the Code a unified whole, such editorial errors are much less likely.

2) Mistakes in the 1954 Code of the sort mentioned above were corrected by acceptance of several proposals, to delete the word "recent" in Articles 32, 35 and 39, thus bringing the requirements for effective publication, description, and typification of fossil plants into line with general botanical requirements. The word "recent" in these articles, by excluding fossil plants, technically made for anarchy in the nomenclature of fossil plants. This situation was not, of course, intentionally created. Apparently the paleobotanical appendix was supposed to have been rewritten at one time in order to cover these exceptions, but was not.

3) In addition to abolition of the former paleobotanical appendix as such, and its incorporation in the main body of the Code, steps were taken to eliminate nomenclatural provisions for fossil plants that are different from those for extant plants, where there is insufficient reason for the difference, and to eliminate from the Code a provision that was not really nomenclatural. It is evident that special provisions for fossil plants tend to cause confusion if they are counter to the general philosophy and practice of botanical nomenclature. Furthermore, there is never any excuse for excess baggage in an already complex Code. For example, Article PB. 2 was deleted on recommendation of the Committee for Paleobotanical Nomenclature, as it merely stated the truism that the rules apply to fossils as well as to extant plants, which fact is already clearly stated in the Preamble to the Code.

4) The one aspect of conforming to normal botanical nomenclatural practice that paleobotanists in 1959 apparently still could not accept was that of Latin diagnosis for new taxa. There was much discussion of the possibility of requiring Latin diagnosis, and a formal proposal was offered. But the Committee for Paleobotanical Nomenclature disapproved strongly the requirement for such diagnosis for fossil plants. Compulsory Latin diagnosis for algae was, however, adopted at the 1954 botanical congress, and fossil algae were (apparently by accident) not specifically excepted from this ruling. Proposals by Mamay (see Table 2) to insert the word recent before algae in the pertinent articles and thus specifically to except fossil algae from required Latin diagnosis had an uneven fate at Montreal. Mamay's proposal to insert the word recent in Article 36 was adopted, but his proposal to insert the same word for the same purpose in part of Article 34 was defeated. However, a subsequent conference of members of the committees for algological and paleobotanical nomenclature found agreement that it had really been the intention of the 1954 Congress to exempt fossil algae from required Latin diagnosis, and a motion was adopted by the Nomenclature Section to this effect. Although the inexact wording of the 1954 Code is retained in the new Code, it is clear that there is no intention that Latin diagnosis be required for fossil algae.

If Latin diagnosis were required for fossil algae, some difficulty would be encountered in relation to plant microfossils previously assigned to the animal kingdom (*Dinophyceae*, *Chrysophyceae*, hystrichosphaerids, silicoflagellates, etc.), for which no Latin diagnosis was provided, because none is required by the zoölogical code of nomenclature, but which microfossils may be transferred to the plant kingdom.

The issue of Latin diagnosis will undoubtedly be subject to further discussion. At this time, just as in 1912 when the exception was originally effected, sentiment among paleobotanists seems, in general to be opposed.

5) Opinion at the general Bureau of Nomenclature sessions, as well as at those of the Committee for Paleobotanical Nomenclature, ran heavily against the conservation of names, despite some eloquent protests, made primarily by applied botanists, against the changing of

TABLE 2

PRINCIPAL RESULTS AFFECTING PALEOBOTANY, OF THE MEETING OF THE INTERNATIONAL BUREAU OF NOMENCLATURE, AT THE NINTH INTERNATIONAL BOTANICAL CONGRESS, MONTREAL, P. Q., CANADA, 16–19 AUGUST, 1959.

A. Proposals accepted that amend paleobotanical provisions of the (1954, Paris) International Code of Botanical Nomenclature (Published by Lanjouw, *et al.*, 1956)

Article in 1954 Code affected	Proposer	Literature reference to proposal	Page in *Synopsis of Proposals**	Effect of proposal, as accepted
Art. 3	C. P. N.**	None	None	Adds note under Art. 3, following definition of organ and form genera: "As in the case of pleomorphic fungi (see Art. 59), these provisions shall not be construed as preventing the use of names of form genera in works referring to such taxa." This note is intended to make it clear that it is permissible to use form generic names in their original sense, even though the type species has subsequently been referred to an organ or natural genus.
Art. 7	Potonié, R.; Schulze, G. M., and G. Buchheim	*Taxon*, 8 (1): 18 *Taxon*, 7 (9): 256	14 14	Alters wording of Art. 7, Note 5, to make it more obvious that genera of plant microfossils, as well as those of megafossils, are organ and form genera.
Art. 10	Staplin, F.	*Taxon*, 7 (8): 226	19	Changes wording of the Note in Art. 10, to make it apply only to recent plants and hence to require type specimens for species of fossil plants.
Art. 10	C. P. N.**	None	None	Adds as a note to Art. 10, to clarify the typification of fossil plants, the following: "The whole specimen used during the establishment of a taxon of fossil plants should be considered the nomenclatural type. If the specimen is cut into pieces (sections of fossil wood, pieces of coal ball plants, etc.), all parts originally used in establishing the diagnosis should be clearly marked."
Art. 32	Traverse, A.; Holm, L.	*Taxon*, 7 (8): 229 *Taxon*, 7 (9): 256–257	39 Traverse and Holm proposals identical)	Makes provisions of Art. 32 regarding effective publication and required description (i.e., valid publication) apply equally to fossil and recent plants.
Art. 34	Mamay, S. H.	*Taxon*, 7 (8): 224	41 (Art. 34, Proposal B only)	Modifies part of Art. 34 to underscore that Latin diagnosis is not required for fossil plants. (Note: Mamay's Proposal C, to modify the rest of Art. 34 in this way, was defeated, but a compromise motion was adopted regarding this proposal which also has the effect of excepting fossil algae from Latin diagnosis.)
Art. 35	Traverse, A.	*Taxon*, 7 (8): 229	42	Makes required typification, Art. 35, apply to fossil plants.
Art. 36	Mamay, S. H.	*Taxon*, 7 (8): 225	43	Makes it clear that required Latin diagnosis for algae mentioned in Art. 36 does not apply to fossil algae.
Art. 36	Schulze, G. M., and G. Buchheim	*Taxon*, 7 (9): 256	43 and 76	Modifies Art. 36 to make it clear that illustration in publication of new fossil plant taxa can be required only for new species and taxa of lower rank, since only these taxa have type specimens. Also modifies Art. PB. 5 (now to be incorporated in Art. 60***) to make it more accurate, showing that a type specimen can exist only for species and taxa of lower rank.

				compromise motion was adopted regarding this proposal which also has the effect of excepting fossil algae from Latin diagnosis.)
Art. 35	Traverse, A.	*Taxon*, 7 (8): 229	42	Makes required typification, Art. 35, apply to fossil plants.
Art. 36	Mamay, S. H.	*Taxon*, 7 (8): 225	43	Makes it clear that required Latin diagnosis for algae mentioned in Art. 36 does not apply to fossil algae.
Art. 36	Schulze, G. M., and G. Buchheim	*Taxon*, 7 (9): 256	43 and 76	Modifies Art. 36 to make it clear that illustration in publication of new fossil plant taxa can be required only for new species and taxa of lower rank, since only these taxa have type specimens. Also modifies Art. PB. 5 (now to be incorporated in Art. 60***) to make it more accurate, showing that a type specimen can exist only for species and taxa of lower rank.
Art. 39	Traverse, A.	*Taxon*, 7 (8): 229	44	Makes provisions of Art. 39, regarding valid publication of genera, i.e., requiring generic descriptions, apply to fossil plants.
Art. 57	C. P. N.**	None	None	Recommendation added under Art. 57: "Fossils uniting diagnostic features of diverse taxa may be assigned either to (1) one [of them], thereby enlarging its circumscription, or (2) may be proposed as a new taxon having the amplified circumscription." There had previously been no directions for such combinations.
Art. 58	Ames, H. T., A. J. Kovar, and G. O. W. Kremp	*Taxon*, 7 (8): 227	59	Deletes example of *Sequoia* Endl. (1847) vs. *Steinhauera* Presl. (1838) as example of precedence of living plant names over fossil plant names. On advice of R. A. Scott, C. P. N.** suggested substitution of the example *Platycarya* Seib. & Zucc. (1843) vs. *Petrophiloides* Bowerbank (1840).
Art. PB. 1; Art. 3	C. P. N.**	None	None	Simplifies definition of form and organ taxa by deleting all but first paragraph of present Art. PB. 1 and adding a single additional paragraph as follows: "An organ genus is a genus assignable to a family. A form genus is a genus unassignable to a family, but may be referable to a higher taxon. Form genera are artificial in varying degree." Revised Art. PB. 1 will be a note following Art. 3***.
Art. BP. 2	C. P. N.**	None	None	Deletes as redundant Art. PB. 2, which explains that the general rules apply to fossil plants.

Art. BP. 2	C. P. N.**	None	None	Deletes as redundant Art. PB. 2, which explains that the general rules apply to fossil plants.
Art. PB. 3	Traverse, A.	*Taxon*, 7 (8): 230	76	Deletes Art. PB. 3. This article had stated that a description would be required for genera or taxa of higher rank on or after 1 Jan., 1953, but was in conflict with Art. 36, which required this on or after 1 Jan., 1912.
Art. PB. 4	Grambast, L.	*Taxon*, 8 (4): 140	None	Deletes as redundant Art. PB. 4, which had defined what are to be considered the types of taxa of fossil plants.
Art. PB. 5; Art. 60	Cross, A. T.	*Taxon*, 8 (4): 139	None	Art. PB. 5 incorporated in Art. 60 of Code***.
Art. PB. 5; Art. 60	Schulze, G. M., and G. Buchheim	*Taxon*, 7 (9): 256	76	Makes it clear that typification by specimen applies only to taxa of specific or lower rank. To be inserted in Art. 60.
Art. PB. 6; Art. 41	Cross, A. T.	*Taxon*, 8 (4): 139	None	Art. PB. 6 incorporated in Art. 41 of Code as a note***.
Rec. PB. 6A; Art. 41	Schulze, G. M., and G. Buchheim	*Taxon*, 7 (9): 256	76	As adapted by C. P. N.**, modifies Recommendation PB. 6A, to recommend that when a new genus of fossil plants is described, the author should state whether he considers it an organ genus or a form genus. For fate of Rec. PB. 6A, see next item.
Rec. PB. 6A; Art. 41	Cross, A. T.	*Taxon*, 8 (4): 140	None	Incorporates Recommendation PB. 6A as a Rec. under Art. 41***.
Rec. PB. 6B	Ames, H. T., A. J. Kovar, and G. O. W. Kremp	*Taxon*, 7 (8): 229	76	Deletes Recommendation PB. 6B, which had reflected a misunderstanding of the type method as applied to form genera.
Rec. PB. 6C; Art. 3	C. P. N.**	None	None	Inserts Recommendation PB. 6C under Art. 3, with wording altered to: "Form genera should not be used as types on which families or taxa of higher rank are established." Deletes note under Rec. PB. 6C which had stated much the same thing as the now modified Rec., but in different words.***
Rec. PB. 6D; Art. 58	Cross, A. T.	*Taxon*, 8 (4): 140	None	Inserts Recommendation PB. 6D in Art. 58 as a Rec., with addition of words "of fossil plants" after "in descriptions of organs."***
Rec. PB. 6F	Traverse, A.	*Taxon*, 7 (8): 230	77	Deletes Recommendation PB. 6F, which had implored paleobotanists to use caution in identifying material. This is not a nomenclatural matter.
Appendix III.	Arnold, C. A.	*Taxon*, 7 (8): 234	81	Conserves the synonym *Cordaianthus* Grand'Eury (1877) over *Botryoconus* Goeppert (1864). *Cordaianthus* is the nearly universally applied name for these cordaitean male inflorescences.

* Lanjouw, J. (Rapporteur general). Synopsis of proposals concerning the International Code of Botanical Nomenclature. Submitted to the Ninth International Botanical Congress. Montreal, 1959. *Regnum Vegetabile*, Vol. 14, 84 pp., 1959, Utrecht.

** C. P. N. = Committee for Paleobotanical Nomenclature of the International Bureau for Plant Taxonomy and Nomenclature of the International Association for Plant Taxonomy. Proposals of the Committee were not published prior to the Congress, as they were a product of the Committee's meetings during the Congress.

*** This was a part of the general incorporation of the former "Appendix II, Special Provisions Concerning Fossil Plants" into the main body of the Code, *per* the proposal of A. T. Cross, *Taxon*, 8 (4): 139–140, 1959.

B. Other actions of the sessions of the International Bureau of Nomenclature directly or indirectly affecting paleobotanical nomenclature.

1. Rejected demands of numerous applied botanists for wholesale conservation of well known plant names that unfortunately are synonyms. Also rejected proposals that commissions be formed, empowered to adjudicate merits of requests for conservation of names. General Committee empowered to receive lists of such requested name conservations, to report on the merits of the lists to the next International Botanical Congress.

2. Declared illegitimate the list of Necker's *species naturales* (originally published in 1790; see proposal by Mansfeld, *Taxon*, 7 (6): 155–156, 1958). These are names that seem to be generic and have often been treated as such. Necker's *species naturales* were not, however, called genera and were not provided with species. They are, hence, regarded as illegitimate, unitary designations (cf. International Code of Botanical Nomenclature – 1956 – Art. 68). This decision might well be taken

Art. PB. 3	Traverse, A.	*Taxon*, 7 (3): 2[illegible]	[illegible]	would be required for genera or taxa of higher rank on or after 1 Jan., 1953, but was in conflict with Art. 36, which required this on or after 1 Jan., 1912.
Art. PB. 4	Grambast, L.	*Taxon*, 8 (4): 140	None	Deletes as redundant Art. PB. 4, which had defined what are to be considered the types of taxa of fossil plants.
Art. PB. 5; Art. 60	Cross, A. T.	*Taxon*, 8 (4): 139	None	Art. PB. 5 incorporated in Art. 60 of Code***.
Art. PB. 5; Art. 60	Schulze, G. M., and G. Buchheim	*Taxon*, 7 (9): 256	76	Makes it clear that typification by specimen applies only to taxa of specific or lower rank. To be inserted in Art. 60.
Art. PB. 6; Art. 41	Cross, A. T.	*Taxon*, 8 (4): 139	None	Art. PB. 6 incorporated in Art. 41 of Code as a note***.
Rec. PB. 6A; Art. 41	Schulze, G. M., and G. Buchheim	*Taxon*, 7 (9): 256	76	As adapted by C. P. N.**, modifies Recommendation PB. 6A, to recommend that when a new genus of fossil plants is described, the author should state whether he considers it an organ genus or a form genus. For fate of Rec. PB. 6A, see next item.
Rec. PB. 6A; Art. 41	Cross, A. T.	*Taxon*, 8 (4): 140	None	Incorporates Recommendation PB. 6A as a Rec. under Art. 41***.
Rec. PB. 6B	Ames, H. T., A. J. Kovar, and G. O. W. Kremp	*Taxon*, 7 (8): 229	76	Deletes Recommendation PB. 6B, which had reflected a misunderstanding of the type method as applied to form genera.
Rec. PB. 6C; Art. 3	C. P. N.**	None	None	Inserts Recommendation PB. 6C under Art. 3, with wording altered to: "Form genera should not be used as types on which families or taxa of higher rank are established." Deletes note under Rec. PB. 6C which had stated much the same thing as the now modified Rec., but in different words.***
Rec. PB. 6D; Art. 58	Cross, A. T.	*Taxon*, 8 (4): 140	None	Inserts Recommendation PB. 6D in Art. 58 as a Rec., with

				note under Rec. PB. 6C which had stated much the same thing as the now modified Rec., but in different words.***
Rec. PB. 6D; Art. 58	Cross, A. T.	*Taxon*, 8 (4): 140	None	Inserts Recommendation PB. 6D in Art. 58 as a Rec., with addition of words "of fossil plants" after "in descriptions of organs."***
Rec. PB. 6F	Traverse, A.	*Taxon*, 7 (8): 230	77	Deletes Recommendation PB. 6F, which had implored paleobotanists to use caution in identifying material. This is not a nomenclatural matter.
Appendix III.	Arnold, C. A.	*Taxon*, 7 (8): 234	81	Conserves the synonym *Cordaianthus* Grand'Eury (1877) over *Botryoconus* Goeppert (1864). *Cordaianthus* is the nearly universally applied name for these cordaitean male inflorescences.

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3. Moved to appoint the following to committees:

a. Committee for Paleobotanical Nomenclature

Chairman: T. M. Harris (U. K.)
Secretary: S. H. Mamay (U.S.A.)
Members: N. A. Bolkhovitina (U.S.S.R.)
P. Corsin (France; declined appointment)
J. W. Funkhouser (U.S.A.; also see below)
W. F. Harris (New Zealand)
L. A. Kuprianova (U.S.S.R.)
S. Leclercq (Belgium; declined appointment)
R. Potonié (Germany)
N. W. Radforth (Canada)
J. M. Schopf (U.S.A.; also see below)
O. Selling (Sweden)
K. R. Surange (India)
A. Traverse (U.S.A.)

b. Editorial Committee — J. M. Schopf (one of ten members)

c. Committee on Neotypes — J. W. Funkhouser (one of seven members)

TABLE 2

tried and true names that unfortunately have turned out to be synonyms. Only one proposal to conserve a fossil plant name was accepted, Arnold's proposal to conserve the synonym *Cordaianthus* Grand'Eury (1877) against the earlier but never used *Botryoconus* Goeppert (1864).

Nor was there much sympathy expressed for the recurring idea of a commission of some sort, empowered to adjudicate the merits of the numerous requests to conserve names. The example of the zoölogical international commission, whose rulings now run to several volumes, seemed especially persuasive against the idea.

6) A development of great significance at the close of the nomenclatural sessions in Montreal was the much strengthened position of paleobotany in general and of paleopalynology in particular. This was especially reflected by the nominees for the important nomenclatural committees that will conduct the affairs of the Bureau of Nomenclature between the Montreal Congress and the next congress, several years hence. Palynologists are on the Committee for Paleobotanical Nomenclature, for the first time in force. No less than eight of the fourteen members are palynologists. Equally important was the naming of a paleobotanist, J. M. Schopf, to the general editorial committee. As will be apparent to anyone who attended the nomenclatural sessions in Montreal, the editorial committee has enormous responsibility. A great many proposals are referred to this committee for final decision as to their appropriateness, or for their proper collation with existing rules. Furthermore, the editorial work in preparation of the new Code is in this committee's hands. Had there previously been a paleobotanist on the editorial committee, obvious errors in the Code affecting paleobotanical nomenclature would have been less likely. Without a paleobotanist on the committee, errors of the sort that had to be painstakingly corrected at Montreal would probably occur again. Paleobotanists should insist, at future congresses, on continuous representation on the editorial committee.

ACKNOWLEDGEMENT

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ABSTRACT

A new spore genus, Pteroretis, *is instituted and a new species of* Acanthotriletes *is described in a study of small spores of upper Chester age in the Texas-Oklahoma Panhandle. Both spores are stratigraphically important.*

Pteroretis, a new Mississippian spore genus

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Sun Oil Company
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INTRODUCTION

In investigations of the plant microfossils from the Anadarko Basin of Texas and Oklahoma, a considerable number of undescribed genera and species have been recorded from deposits of Chester, Morrow, and post-Morrow age. One of the most prominent has been a spore from the upper Chester that is morphologically unique and which has been given the generic designation *Pteroretis*. A second spore, assignable to the genus *Acanthotriletes*, is quantitatively so significant that its inclusion is considered advisable in this treatment.

Both spores are components of excellent spore assemblages of the upper Chester. *Pteroretis* is a sparse but conspicuous representative and appears to be limited to the upper Chester in the area of study. The *Acanthotriletes* does not have such a narrowly restricted occurrence and has been recorded from several localities where it is not associated with *Pteroretis*. However, it is dealt with here in view of its high incidence in some assemblages with *Pteroretis*.

ACKNOWLEDGMENTS

The authors wish to thank the Sun Oil Company for permission to publish, and Mr. Edward Davidson for assistance with illustrations.

SYSTEMATIC DESCRIPTIONS

Anteturma Sporites H. Potonié, 1893
Turma Triletes Reinsch, 1881
Genus **Pteroretis** Felix and Burbridge, **new genus**

The spore consists of two parts, an outer (perisporal) membrane and the body proper, which is included within the perisporal membrane. The spore is characterized by the possession of six prominent wings (text-fig. 4). These represent expansions of the perisporal membrane, which is very thin and is continuous in the area between the wings. The wings are large and spreading, but their structure suggests that they were probably quite delicate. They are thin, consisting of a single layer, and somewhat filmy; they are usually observed variously collapsed or folded. The tendency to fold or crumple gives rise to variable appearances, and it is usually difficult to discern six wings on a specimen. This is due in part to orientation of the spore and in part to the membranous nature of the wings, for the widely flared appendages may possess several folds, and they often overlap. The wings are attached to the perisporal body throughout their length, and they arch out, frill-like, beyond the body at both the proximal and distal ends (text-fig. 1). They have a much more pronounced extension beyond the distal end than over the proximal, but the proximal extension is usually sufficient to obscure the trilete rays. The wings possess a delicate network of veins, which occasionally anastomose but without any apparent regularity. The trilete rays are indistinct, usually being obscured by the perisporal membrane or the folded wings. They are a feature of the body proper and are not visible on the perispore. That portion of the perispore membrane between the wings and extending over the spore body both proximally and distally is characterized by a series of prominent, thickened, more or less parallel ridges (pl. 1, fig. 7). These join the thick attachment ridge formed at the juncture of wing and perisporal membrane. This system of transverse ribs or ridges is a part of the perispore, and the entire membranous outer coat, including wings, is often observed free of the inner spore body (pl. 1, figs. 1, 8). The ridges occasionally bifurcate but do not appear to have any regular pattern of division (pl. 1, fig. 7).

The entire spore with wings expanded is approximately spheroidal but is usually observed more or less flattened and with the wings folded over, overlapping each other. The wings are seated on a thickened ridge, running proximally-distally. The mode of insertion of the vein on the basal ridge is illustrated in text-figure 2. The vein narrows after about 5μ and is normally 1–2μ in width throughout most of its length.

Pteroretis primum Felix and Burbridge, **new species**
Plate 1, figures 1–8; text-figures 1–2, 4

Holotype: (nominifer): Sun Oil Company paleontological collections, Slide 692B–1, location 40.2 × 111 (Ref. 17.4 × 117) (pl. 1, fig. 2). In agreement with the views expressed by Schopf (1960), it is believed that the holotype serves only a nomenclatural function. This is especially true in plant microfossil studies, where a single specimen seldom can conceivably include all the characters of a taxon. The specimen designated as the holotype (pl. 1, fig. 2) is merely the spore with which the name is permanently associated. It does not show all of the diagnostic characteristics of the new genus, and the "nominifer" method seems to afford a more logical comprehension of its function.

Occurrence: From standard core at 8899 ft. and 8915 ft. in the Sun Oil Company Theresa Wright #1 well, Ochiltree County, Texas (Sec. 3, Blk. 13, T & N. O. Survey).

Diagnosis: The recorded over-all diameter is 100–130μ in relatively undistorted specimens. The body of the spore, exclusive of the perisporal membrane, is spherical and ranges from 55μ to 72μ in diameter. The width of the prominent ridge to which the wings are connected is about 4μ, and its height 1.5–3μ. The wing veins originate from this ridge, and the veins themselves are enlarged at their bases and begin to decrease in thickness about 5μ from the point of basal attachment. The enlarged vein base is 1.5–2.2μ wide parallel to the polar axis and 3.2–4.8μ wide parallel to the equatorial axis. Distance between veins on the attachment ridge is 2.2–3μ. Wing width varies but is maximum in the equatorial area, where it is 30–35μ when the wing is fully expanded; it is about 20μ at the distal pole. The transverse ribs encompassing the central body are 2μ wide and 4–6μ apart. Trilete rays are extremely difficult to discern and are usually covered by the perisporal membrane and its pattern of thickened ridges; the crumpled and folded wings may further obscure the sutures. The trilete germinal opening is visible in a few specimens (pl. 1, fig. 3); the rays are relatively short, averaging about 16μ in length.

Comments: Pteroretis does not bear a close resemblance to any described Paleozoic spore. In its usual distorted condition it sometimes suggests *Alatisporites*, but the resemblance is only superficial. The appendages of *Alatisporites* are bladders or air sacs, with the point of attachment in the interradial area. There are three, six, or eight bladders in described forms, with occasional variants having as many as eleven. There is only one record of *Alatisporites* with bladders extending beyond the proximal or distal end; Guennel (1958) described *A. pottsvillensis* with three bladders attached at the interradial margin and bulging out beyond the spore's periphery to meet distally. The bladder ornamentation of *Alatisporites* is levigate, granulose, or punctate, and the branching veins characteristic of the *Pteroretis* wing have not been observed in *Alatisporites*.

It is a common practice among investigators to use the terms "bladder" and "wing" interchangeably, and in some cases "flange" is also used synonymously to refer to the prominent appendages of plant microfossils. The senior author has also followed this pratice in published descriptions, but the unique appendages of *Pteroretis* have necessitated reconsideration of the usage of such descriptive terminology. The appendages of *Pteroretis* are designated as wings because the term "bladder", properly speaking, refers to a membranous sac or a distended membranaceous appendage. This designation of the appendages is correct in referring to such entities as *Alisporites*, *Pityosporites*, *Florinites*, or *Parasporites*. However, the appendages of *Pteroretis* are composed of a single thickness and are not sac-like or inflated, and "wing" thus appears to be the more accurate appellation. "Flange" refers to an encircling rib or rim about a spore body, such as that in *Densosporites*, and it is often improperly used in describing specimens of gymnospermous affinities.

One of the most numerous of the spores encountered in these investigations of the upper Chester is a small spinose form assignable to *Acanthotriletes*. The distinction between *Acanthotriletes*, *Apiculatisporites*, and *Lophotriletes* is very slight and is based primarily upon the nature of the spines. However, the Panhandle entity should be included in *Acanthotriletes* as treated by Potonié and Kremp (1955).

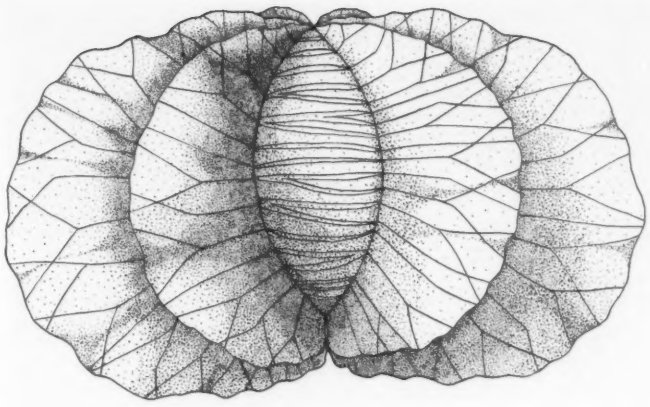
Turma TRILETES Reinsch, 1881
Subturma AZONOTRILETES Luber, 1935
Infraturma APICULATI (Bennie and Kidston, 1886)
R. Potonié, 1956
Genus ACANTHOTRILETES (Naumova, 1937)
Pontonié and Kremp, 1954

Acanthotriletes uncinatus Felix and Burbridge, **new species**
Plate 1, figures 9–10; text-figure 3

Holotype (*nominifer*): Sun Oil Company paleontological collections, Slide 695B–1, location 25×115.6 (Ref. 18.7×116.1) (pl. 1, fig. 9).

Occurrence: From standard core at 8899 ft., 8911 ft., and 8915 ft. in the Sun Oil Company Theresa Wright #1 well, Ochiltree County, Texas (Sec. 3, Blk. 13, T & N. O. Survey); from core at 9148 ft. and 9151 ft. in the Magnolia Petroleum Company Roy Linn #1 well, Ochiltree County, Texas (Sec. 653, Blk. 43, H. & T. C. Survey); and from core at 7428 ft. in the Sun Oil Company David Penner #1 well, Beaver County, Oklahoma (Sec. 12, 2 N, 20 ECM).

Diagnosis: Spores radial, trilete, spherical; body wall thin and usually possessing minor folds; ornamentation consisting of minute, falcate spines, with tips slightly tapered, the spines 1–2.5μ long (1.5μ average), averaging 1μ in diameter, and spaced about 3μ apart; trilete rays indistinct, obscured by spines and folds in wall, not exceeding 10μ in length; spore size ranging from 25μ 42μ, average diameter 30–35μ.



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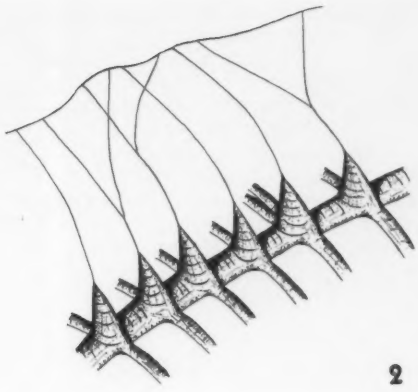

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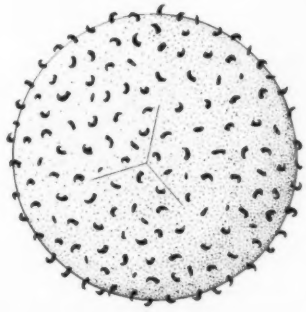

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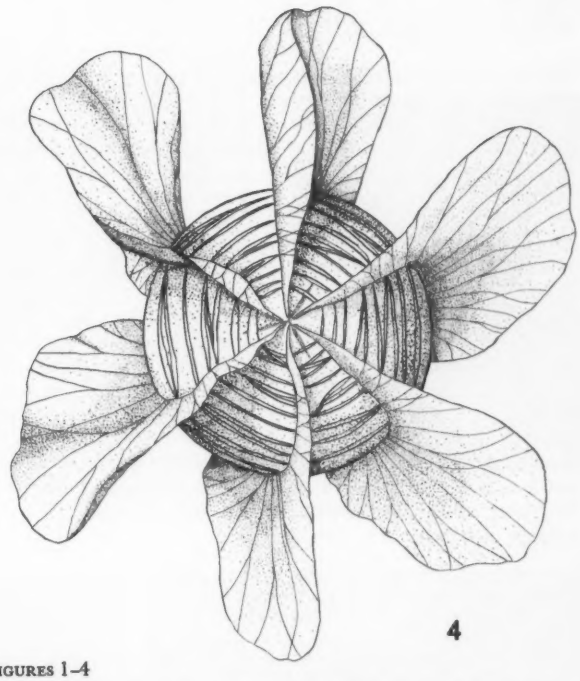

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TEXT-FIGURES 1–4

1–2, 4, *Pteroretis primum* Felix and Burbridge, n. sp. 1, Spore in axial (longitudinal) section; 2, detail of wing section, showing basal attachment ridge and its union with body ridges and the flared bases of the wing veins; 4, spore in equatorial (transverse) section, showing proximal pole and wing insertion; 3, *Acanthotriletes uncinatus* Felix and Burbridge, n. sp., spore in equatorial (transverse) section, showing proximal area.

Comments: Acanthotriletes uncinatus resembles *A. ciliatus* Pontonié and Kremp, 1955, but lies well outside the size range of the latter. The trilete rays of *A. ciliatus* are more pronounced, and the body is more densely covered with spines. The kooked nature of the spine tip is not recorded as a feature of *A. ciliatus*. *A. uncinatus* compares in size with *A. echinatus* Hoffmeister, Staplin, and Malloy, 1955, and the latter has some spines with hooked tips. However, the spines of *A. echinatus* are very densely crowded, and the hooked tip is not a diagnostic feature, as it appears to be in *A. uncinatus*.

Table 1 shows the percentages of the principal spore genera in the cored interval within which *Pteroretis primum* and *Acanthotriletes uncinatus* occurred in the Sun Theresa Wright #1 well. These percentages are based

on a minimum of 200 specimens counted per sample. The presence of *Tripartites*, *Rotaspora*, and *Schulzospora* is characteristic of Mississippian sediments, and this type of assemblage has been noted in every occurrence of *Pteroretis primum* or *Acanthotriletes uncinatus*.

TABLE 1

STATISTICALLY PROMINENT UPPER CHESTER SPORE GENERA IN THE SUN OIL THERESA WRIGHT # 1 WELL, OCHILTREE COUNTY, TEXAS.

Depth	*Lycospora*	*Densosporites*	*Punctatisporites*	*Tripartites*	*Rotaspora*	*Schulzospora*	*Acanthotriletes uncinatus*	*Pteroretis primum*
8899 ft.	60.0	12.5	13.5	1.0	0.5	0.5	0.5	2.0
8911 ft.	1.0	4.0	12.0	1.0	–	27.0	32.5	–
8915 ft.	32.0	8.0	8.0	2.0	0.5	5.0	25.0	2.0

The slides used are all mixed mounts, and so that other investigators may easily locate the types and other illustrated specimens on these slides, the exact field position of the specimens are noted in the text and plate explanations as coordinates, in parentheses, followed by a reference point coordinate for each slide. A microscope with mechanical stage and vernier scale in millimeters is required. Traverse (1958, 1960) and Pierce (1959) have explained methods of coordinate conversion with the use of a given reference point. The Sun Oil collections are calibrated on a Leitz Ortholux microscope mechanical stage to tenths of millimeters. The horizontal (smaller) reading is listed before the vertical (larger). Scales on different mechanical stages sometimes run in opposite directions, and Pierce (1959) has devoted special attention to this factor. To facilitate location still further, especially when a vernier scale is not available, each specimen has been oriented at the midpoint of a circle drawn with a diamond-pointed ringing objective.

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PLATE 1

1 *Pteroretis primum* Felix and Burbridge, n. sp. Perisporal portion of spore with inner spore body absent, × 500; Slide 692B–11, location 8.8×109 (Ref. 31.8×117.6).

2 *Pteroretis primum* Felix and Burbridge, n. sp. Holotype, oblique polar view of distal side, × 500; Slide 692B–1, location 40.2×111 (Ref. 17.4×117).

3 *Pteroretis primum* Felix and Burbridge, n. sp. Oblique view of proximal side, showing opened trilete, × 500; Slide 692B–9, location 18.2×124.8 (Ref. 31.2×117.2).

4 *Pteroretis primum* Felix and Burbridge, n. sp. Model reconstruction of spore, showing oblique distal view.

5 *Pteroretis primum* Felix and Burbridge, n. sp. Oblique view of distal side, × 500; Slide 692B–4, location 39×127 (Ref. 19×116.6).

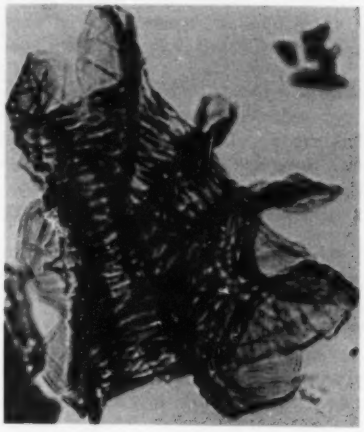
6 *Pteroretis primum* Felix and Burbridge, n. sp. Detail of wing, showing attachment line and veins, × 750; Slide 692B–5, location 6×122 (Ref. 29.5×118.8).

7 *Pteroretis primum* Felix and Burbridge, n. sp. Central perispore with wings detached, showing transverse ribs, × 750; Slide 692B–5, location 7.2×125.9 (Ref. 29.5×118.8).

8 *Pteroretis primum* Felix and Burbridge, n. sp. Perisporal membrane with inner body absent, × 500; Slide 692B–5, location 6×122 (Ref. 29.5×118.8).

9 *Acanthotriletes uncinatus* Felix and Burbridge, n. sp. Holotype, × 500; Slide 695B–1, location 25×115.6 (Ref. 18.7×116.1).

10 *Acanthotriletes uncinatus* Felix and Burbridge, n. sp. × 500; Slide 692–9, location 22.9×123 (Ref. 33.1×118).



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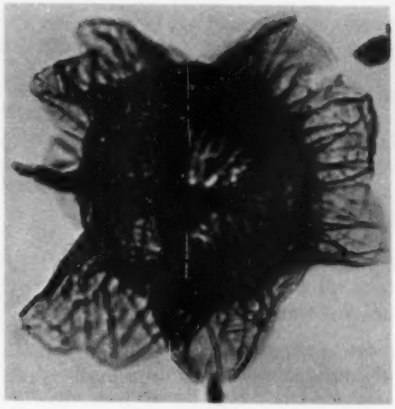

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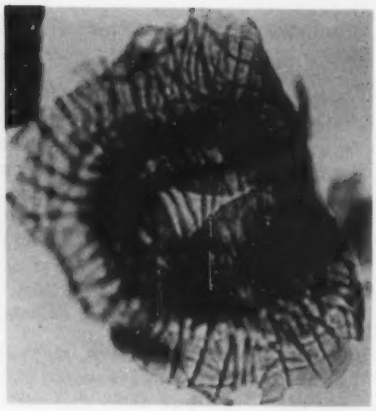

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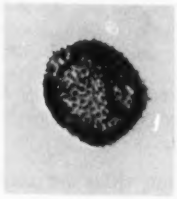

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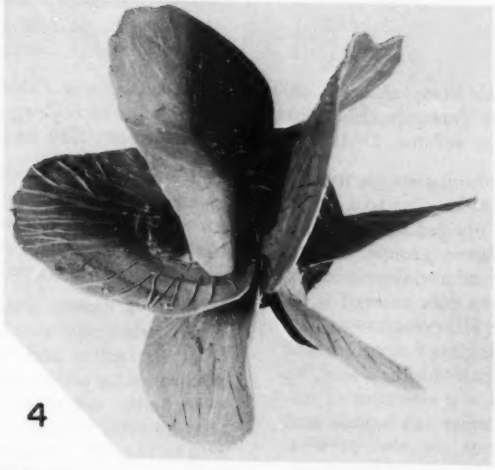

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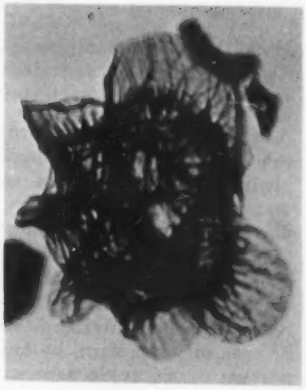

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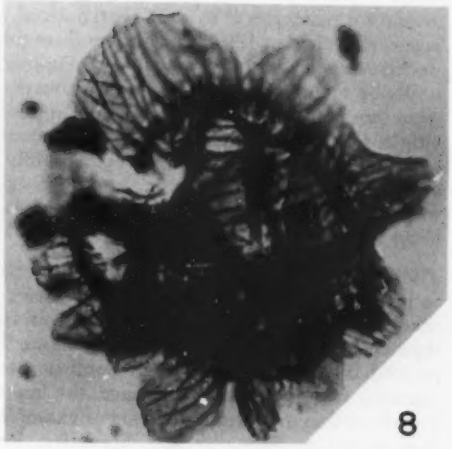

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Reviews

HEINRICH HILTERMANN: *Bibliographie stratigraphisch wichtiger mikropaläontologischer Publikationen von etwa 1830 bis 1958 mit Kurzreferaten.* E. Schweizerbart'sche Verlagsbuchhandlung (Nägele und Obermiller), Stuttgart W, 1961. Issued in five volumes of 80 pages each; price per volume, DM 18.80 ($4.70); complete, DM 94 ($23.50).

A very large number of micropaleontologists are unable to afford themselves the "luxury" of keeping to a single phylum and from time to time are obliged to work with material belonging to widely different groups. This is particularly so for the industrial micropaleontologist. One of the major stumbling blocks encountered is, of course, the literature problem. Dr. Hiltermann has had these people in mind when compiling his five volumes of references on stratigraphic micropaleontology and, as he says in his preface, he has made a selection of important stratigraphic papers, the more taxonomic and phylogenetic works being left out for the present. Naturally, in a work consisting of selections of literature, it is to be expected that another author might have made a somewhat different choice. However, the most important papers seem to have been noticed, and as it is proposed to issue additional volumes from time to time, we may expect that any important omissions will eventually be included. Even so, it is not always clear as to what norms for selection have been applied. For example, the rather cruel omission of Erdtmann's "Literature on Palynology" from the section on bibliographies and the omission of Skogsberg's and Elofson's classic works on the ostracods while certain zoologic works of lesser standard are cited.

There are a few formal points the reviewer would like to point out. For the most part the printers have used the fused form of "tz" (ʦ) in names, but this is not done rigorously. For example one finds the name Wetzel also printed Weʦel. This is certainly confusing to the non-German user. Secondly, we have the matter of the transliteration of Russian names. For example, Швейер is rendered as Schwejer and Schweier, Рейтлингер as Rejtlinger. Moreover, Russian titles are sometimes given in German translation and sometimes only in transliterated form. These points are, however, of a very minor nature and in no wise detract from the overall good impression made by the publication.

Volume 1 covers textbooks, generalia and bionomy. Useful additions here in the future would be the work of G. Arrhenius and K. G. Nyholm. As an example of the groups on which titles are presented we may mention bryozoans, conodonts, foraminiferans, radiolarians, charophytes, echinoids, and even graptolites. Here, as also in the other volumes, the coverage of the Russian literature is particularly satisfactory. Techniques and methods of study are also treated in the first volume and a beginning is made on the Paleozoic. The second volume continues with the Permo-Carboniferous, and then treats Triassic, Jurassic and some of the Cretaceous, the coverage being very full. Volume 3 supplies generally a well chosen set of titles on Cretaceous and Tertiary Volume 4 continues with Tertiary literature, (article 2320 seems to be wrongly placed), and volume 5 lists Quaternary works. This volume is concluded with a list of bibliographic works, an index of authors, and a subject-matter index.

The reviewer finds the layout of the work praiseworthy and the procedure of supplying short comments on the contents of the papers most useful. Dr. Hiltermann's bibliography fills a long existing gap in the arsenal of the stratigraphical micropaleontologist.

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HANS E. THALMANN: *An index to the genera and species of the Foraminifera, 1890–1950.* George Vanderbilt Foundation: Stanford University, Stanford, California, 393 pages, 1960. Price: $10.00 plus postage.

This newly published volume supplies students of the foraminifera with an invaluable tool. Similar in style to the annual indices to the genera and species of foraminifera published by Thalmann for many years, it covers all newly proposed generic and specific names appearing between 1890 and 1950.

In 1955, Charles Davies Sherborn's "An index to the genera and species of the Foraminifera" covering the genera and species described through 1889, long out of print and difficult for foraminiferal workers to obtain, was reprinted by the Smithsonian Institution. The lack of complete coverage of foraminiferal literature after 1890 by a comprehensive index remained a serious lack to workers in this field. Students of foraminifera now owe a debt of gratitude to Hans E. Thalmann for continuing the earlier work of Sherborn and completing an index of genera and species for the 60 year period 1890 through 1950, and to the George Vanderbilt Foundation at Stanford University for undertaking the publication of this important volume. Thalmann's index is published in an attractive, well printed, double columned quarto volume. The following data are given for generic names: reference, type species, family assignment and geologic age; for species; the reference, geologic age and area from which described are given. The generic and specific names are printed in bold face type for easier visibility. Some references for years prior to 1890 are also given when these were not included in the Sherborn index.

A complete coverage of the well scattered foraminiferal literature through 1950 is now available in two volumes, the Sherborn index through 1889, and the Thalmann index through 1950. The new volume may be obtained from the George Vanderbilt Foundation at Stanford University.

ALFRED R. LOEBLICH, JR.
California Research Corporation
La Habra, California

Back volumes of Micropaleontology

Volumes 1–6 of MICROPALEONTOLOGY are still available at $16.00 per volume. Subscribers wishing to fill in gaps in their file of this publication should do so without delay. Once the supply has been exhausted, it cannot be renewed because of prohibitive costs.

Some single numbers are still available at $4.00 each.

THE EDITORS

news reports

ARGENTINA

ESTEBAN BOLTOVSKOY

This report covers activities in micropaleontology in Argentina and Uruguay since my last report published in April, 1960. As usual, I shall arrange my report according to the groups of organisms discussed.

FORAMINIFERA

Dr. H. Camacho of the Universidad de Buenos Aires has finished the installation of a micropaleontological laboratory in the Department of Geology of the University. This laboratory is of great importance as it will permit the training of students not only in theoretical, but also in practical micropaleontology. It will aid in the preparation of new micropaleontologists in the same University without sending them for training to other institutions. Dr. Camacho has given a course in micropaleontology for some time. He is now working on a manual of fossil invertebrates in which some chapters will be devoted to micropaleontological problems. He plans to finish this manual by the close of 1961. In addition, Dr. Camacho is preparing a manuscript on the Eocene foraminifera of Tierra del Fuego which will probably be published this year.

The following short lines were communicated by Dr. J.P.H. Kaasschieter of the micropaleontological staff of the Shell Production Company of Argentina, Ltd. (Shell CAPSA). Shell's stratigraphic section is headed by Dr. Haak. His professional staff consists of Dr. J.P.H. Kaasschieter and two assistants. The section is engaged in the normal routine type of work, especially in the study of well samples from the southern part of the Province of Buenos Aires and the eastern part of the Province of Rio Negro. The present studies are mainly concerned with foraminifera and ostracoda of Tertiary (Paleocene and Mio-Pliocene) age.

I am very happy to report that we have every hope to expect the development of research activity in foraminifera in Uruguay in the near future. Dr. J. C. Martinez Machiavello of the Museo de Historia Natural in Montevideo is now in charge of the Geological and Paleontological Section of the Museum. In 1959 he spent many months at the University of Milan where he received training in micropaleontology. At present Dr. Martinez Machiavello is occupied with the collection of foraminiferal samples from the Atlantic Coast, as well as along the coast of the Rio de la Plata. He intends to begin their study this year.

Your correspondent, working at the Museo Argentino de Ciencias Naturales "B. Rivadavia," Buenos Aires, published during the past year the following three papers: "La línea de Convergencia Subantartica y su estudio en base a los Foraminiferos (Serv. Hidr. Naval, Misc., Publ. no. 1018), "Los Foraminíferos de los Sedimentos Cuaternarios en los alrededores del Puerto Quequén" (Rev. As. Geol. Argentina, vol. 14, no. 3/4), and "Problemas de la Ecología Química en la Argentina" (Cienc. Invest., 1961, no. 4). Problems relating to the use of foraminifera as biological indicators of marine currents continues to interest me. For its better investigation, I undertook a special voyage on board the oceanographic ship *Capitán Cánepa* just in the region where the convergence zone takes place. I was able to determine immediately the character of the waters (sub-antarctic, subtropical or coastal zone) by studying planktonic forams collected by net, and, in this way, to direct, with the specialist on physical oceanography, the course of our ship. This voyage was extremely interesting and testified once more that planktonic foraminifera are of great value as biological indicators. It was possible to define the zone in question many times with great exactitude on the basis of the foraminifera present. In addition, I am occupied at the present time in the study of material collected near two marine biological stations in Argentina, namely, the station at Quequén (Province de Buenos Aires) and at Puerto Deseado (Patagonia). Both places have a very interesting fauna from the biological point of view.

TINTINNIDS AND DINOFLAGELLATES

These two groups are being studied solely by Dr. E. Balech (Quequén, Province de Buenos Aires). The main object of his extensive and very productive studies concern the Recent representatives of these two groups. The following studies should be listed as finished and published: "Tintinnoinea del Mediterráneo" (Trab. Inst. Español Oceanogr., No. 28), this paper has extensive descriptions of 60 species with their complete synonymy as well as 22 plates; "Operación Oceanográfica Merluza, Crucero 5" (Serv. Hidr. Naval Publ. No. 618), this paper is confined to a study of the dinoflagellates, and contains the descriptions of new species and discussions on their significance as biological indicators. The discussion on the value of plankton

as a biological indicator is also found in a very interesting work by the same author entitled "The change in the Phytoplankton population off the California Coast" (Calif. Coop. Ocean. Fisher. Res., vol. 7, sect. 2). Besides these three papers the following three communications were published by Dr. Balech in "Symposium sobre plancton," (Centro de Cooper. Cient. de UNESCO, Montevideo, 1958): "Evolución general de los estudios de Dinoflagellados y Tintinoineos," "Exploración planctónica del litoral bonaerense" and "Los Dinoflagelados y Tintinnoineos como indicadores oceanográficos." The following studies should be mentioned as in process of preparation by this very industrious student: "Plankton of the Scripps Institution Expeditions *Norpac* and *Downwind*"; the author was able to determine approximately 250 species of Dinoflagellates and Tintinnids and an interesting relationship between their geographic distribution and living conditions. "Plankton of Quequén"; some new species (at least for the western Atlantic) have been found and described; "Some interesting planktonic samples from the Ecuador coast and Galapagos Islands"; "Plankton taken near the Drake Strait on both sides of the Atlantic Convergence line," and a rather extensive work on the tabulation of the different genera of Dinoflagellates (especially *Peridinium*). This study has as its final task the revision of the systematics of this complicated and little known group.

DIATOMS

The Uruguayan specialist in diatoms and phytoplankton in general, Dr. H. J. Ferrando of the Servicio Oceanográfico y de Pesca, Montevideo has published two papers dealing with this group: "Frecuencia estacional del Microplancton costero de Montevideo durante el año 1958" (Ann. Fac. Vet. Uruguay, vol. 9, no. 7) and "Frecuencia estacional del Microplancton costero de Montevideo durante el año 1959" (Publ. Cien. S.O.Y.P., Contr. Pianc.) At present he is studying the seasonal frequency of the phytoplankton, especially diatoms, near Lobos Island and Punta del Este. This study promises to be very interesting, not only from a purely scientific point of view, but also from a practical one, as it is closely connected with the fish hauls made there. In addition, Dr. Ferrando undertook some time ago the direction of the Planktological Section of the newly organized S.O.Y.P. (Servicio Oceanográfico y de Pesca). This undoubtedly will considerably stimulate the activity of planktological studies in this part of the Atlantic Ocean.

SPORES AND POLLEN

Dr. S. Archangelsky of the Instituto M. Lillo, Tucumán, Argentina has spent many months in Great Britain, having been awarded a fellowship from the British Council. At Glasgow and Reading Universities he studied pollen grains belonging to male cones of the Araucariaceous type, which had been found in the Ticó Formation (Upper Jurassic) in Santa Cruz Province, Argentina. The description of these grains will be published during 1961. Other pollen grains and spores have been found in strata containing *Rhacopteris ovata* of Carboniferous age. The presence of a monosaccate type of grain, rather similar to *Florinites*, presents a delicate stratigraphical problem, concerning the correct dating of the Argentine Carboniferous formations, which have so far been considered Lower Carboniferous in age. The study of the pollen and the spore content of these formations will probably give the answer to this problem.

Dr. Martinez Machiavello, already mentioned above, received a month's training in pollen and spore analysis at the University of Pisa. He intends to begin the study of fossil spore and pollen material from the strata of Uruguay.

OTHER NEWS

The Argentine Geological Congress took place in San Juan, Argentina, in November, 1960. Many delegates from all parts of Argentina as well as some foreign students attended. Dr. Camacho read a paper on the Eocene foraminifera of Tierra del Fuego.

At the same time the Argentine Zoological Congress was held in Tucumán. Your correspondent presented and read his investigations relating to the problem of chemical ecology in our country, mainly based on the study of foraminifera.

We greatly enjoyed the visit of Dr. D. Closs of the Universidad do Rio Grande do Sul, Porto Alegre, Brasil, who spent a few days in our Museum studying his material and comparing it with our collections.

ESTEBAN BOLTOVSKOY
Museo Argentino de Ciencias Naturales
Buenos Aires

AUSTRALIA

IRENE CRESPIN

Your correspondent was overseas for a few months during 1960 on an extended holiday. However, she managed to visit laboratories in Miami, U.S.A. and in England and Holland.

Probably the largest international gathering of micropalaeontologists ever assembled together was at the International Geological Congress in Copenhagen, and the writer had the privilege of meeting many colleagues with whom she had corresponded for many years.

The work of micropalaeontologists in Australia has increased greatly with the intensified search for oil in this country. New discoveries and new problems are appearing with the examination of samples from each new bore.

The micropalaeontologists of the Bureau of Mineral Resources in Canberra, are employed continuously on the study of outcrop and surface rocks collected by Bureau geologists and by private companies engaged in the search for oil in all parts of Australia. The foraminifera continue to be the responsibility of D. J. Belford and the writer. The latter has worked primarily on the Lower Cretaceous foraminiferal assemblages in the rocks of the Great Artesian Basin. She has recently published in the Report series of the Bureau (Report No. 54) a list of types and figured specimens of all fossils in the Commonwealth Palaeontological Collection at Canberra. This comprises more than 3,000 specimens. D. J. Belford is continuing his studies of the foraminifera of the Mesozoic and Tertiary of Australia and New Guinea. A paper on the Miocene and Pliocene planktonic Foraminifera of Papua and New Guinea is now in press.

Dr. P. R. Evans is at present studying the microplankton and spore assem-

blages in the Permian and Mesozoic sequences in the different sedimentary basins of Australia. Many excellent suites of microplankton and spores have been obtained from subsurface sections, and fairly satisfactory results of long range correlations are being obtained. It is hoped that his interesting discoveries will be recorded at an early date.

P. J. Jones continued his study of Devonian and Carboniferous Ostracoda, and a paper is in press on the "Distribution of the genus *Cryptophyllus* in the Upper Devonian and Carboniferous of Western Australia." He has now undertaken the investigation of conodonts which are being found in unexpected abundance in the Lower Palaeozoic rocks of Australia.

Dr. Glaessner, of the University of Adelaide, continues his work on general palaeontological problems, and his recent work on the Tertiary Decapoda of New Zealand has just appeared.

Many palaeontologists will remember his interesting contribution on Precambrian fossils in South Australia at the Congress. Several students of the foraminifera are doing post graduate study under his guidance. Dr. Mary Wade continues her investigations of Tertiary foraminifera. Dr. N. H. Ludbrook of the Mines Department of South Australia is doing palaeontological work for that organization and is reporting on the foraminifera from many bores drilled in that State.

In Queensland, Dr. N. de Jersey is making palynology investigations for the Geological Survey. He is, at present, studying the boundary of the Triassic-Ipswich coal measures.

Dr. I. Cookson of the University of Melbourne, is still engaged on the study of both microplankton and spores. The investigation of spores in the Mesozoic stratigraphy of Victoria is producing results, in that deposits previously considered to be of Jurassic age are now considered to be Lower Cretaceous. Miss Mary Dettmann is now at Cambridge University, where she has been studying Australian Triassic megaspores. J. T. Douglas is working on microplankton and spores for the Geological Survey of Victoria, and D. Taylor is studying the foraminifera. Dr. A. C. Carter, formerly of that organization, is now lecturer in palaeontology in the University of New South Wales in Sydney.

Dr. B. E. Balme, of the University of Western Australia, continues his palynology studies. He has a paper in press on spores from the Devonian of Western Australia. Dr. P. J. Coleman of the same University, has been working on the Tertiary foraminifera from the Solomon Islands.

Dr. F. Kicinski, of British Petroleum Ltd., has returned to London from Port Moresby, Papua, as this company has ceased, at least for the time being, to carry out detailed palaeontological investigations in its search for oil in that region.

IRENE CRESPIN
Bureau of Mineral Resources
Canberra, Australia

CANADA

FRANK L. STAPLIN

This correspondent is grateful to M. J. Copeland, G. E. Rouse, and J. H. Wall for the reports from the Geological Survey of Canada, The University of British Columbia, and the Research Council and University of Alberta, respectively.

GEOLOGICAL SURVEY OF CANADA (OTTAWA)

M. J. Copeland is continuing study on Ostracoda from the Maritimes, and Gaspé and Anticosti areas of Quebec. His paper on Silurian species from Arisaig, Nova Scotia (Palaeontology 3, no. 1) will be followed by a further, paper, also including material from elsewhere in Nova Scotia and New Brunswick. Contributions are in preparation on Lower Devonian ostracods from the St. Alban and St. Leon formations, Dalhousie, New Brunswick, and on Ordovician faunas, Lake Timiskaming area, Ontario. This year, the Royal Society of Canada will publish his paper on Kinderhook microfossils, Crowsnest Pass, Alberta. Work is continuing on Jurassic Ostracoda of the Plains region.

Permo-Carboniferous palynological studies are under the direction of P. A. Hacquebard. During 1960, the bulk of these studies were related to drilling programs conducted in the Pictou and Springhill coalfields, Nova Scotia. Spore histograms of the coal seams have been prepared by J. R. Donaldson and M. S. Barss to assist in correlations and structural interpretations.

Spore analyses of New Brunswick Pennsylvanian coals are being used to establish stratigraphic relationships. A thin coal near Shediac, New Brunswick, containing spores indicative of Stephanian age, has been correlated with a bore hole assemblage on Prince Edward Island from a depth of 1900 feet. These are the youngest Carboniferous rocks so far reported from the Maritimes.

Lower and Middle Devonian proximally-ribbed spores will be described by D. C. McGregor in a bulletin of the Geological Survey of Canada. Other papers nearing completion describe microfossils from the Ordovician Red River formation of Manitoba, and spores from the Ghost River formation type section of Alberta (with R. D. Greggs and G. E. Rouse). McGregor is also preparing reports on Devonian microfloras from the James Bay Lowland of Ontario and the Gaspé of Quebec.

J. Terasmae has completed fieldwork for a report on Pleistocene deposits of Ontario. The purpose of the work is to establish the chronology of Pleistocene and post-glacial deposits and events within the Province. Several radiocarbon age determinations support the palynological studies. A radiocarbon laboratory has been established recently at the Geological Survey. Palynological studies of Pleistocene and Tertiary deposits of the Canadian Arctic are continuing, with emphasis on stratigraphic correlation.

RESEARCH COUNCIL OF ALBERTA
UNIVERSITY OF ALBERTA (EDMONTON)

Research projects in micropaleontology and palynology of these two organizations are integrated to a considerable degree, and are here presented in combined form.

In the University, Miss W. McKay is completing her study of Mississippian foraminifera from Western Alberta, under the auspices of the Research Council. Sediments of glacial Lake Regina, Saskatchewan are being studied by D. Delorme. Ostracods, charophytes, fern sporangia and micro-vertebrates

are being used in efforts to determine depositional history, correlations, and climatic and ecologic conditions during the late Wisconsin glaciation. C. Singh, doctoral candidate from India, is working on plant microfossils of the Lower Cretaceous Mannville group of central Alberta. This project is supported by the Fuels Branch of the Research Council and is under the direction of their Paleobotanist, J. D. Campbell. J. D. Wall is giving the course in micropaleontology in the Geology Department of the University, in the absence of Prof. C. R. Stelck, who is on sabbatical leave in Australia.

Dr. Campbell, of the Research Council, is working on the palynology of the Ardley member of the Upper Cretaceous Edmonton formation, and on fossil woods of the Edmonton formation and other deposits in northwestern Canada. R. Green is preparing a paper on the ostracods of the Mississippian Banff formation. "Upper Cretaceous Foraminifera from the Smoky River area, Alberta", by Dr. Wall, has been published as Research Council of Alberta Bulletin 6. Saskatchewan Dept. of Mineral Resources Bull. 53 (in press) will contain his paper, "Jurassic microfaunas from Saskatchewan." He has collected additional sections in his study of Upper Cretaceous Wapiabi microfaunas of the Alberta Foothills.

UNIVERSITY OF BRITISH COLUMBIA (VANCOUVER)

Dr. G. E. Rouse, Department of Botany, is using plant microfossils to correlate Eocene deposits of isolated basins in interior British Columbia. He has submitted a paper on the Burrard formation, Vancouver area, to Micropaleontology. Mr. G. Kiss has finished his M. Sc. thesis on post-glacial pollen and spores from a Vancouver area peat. Miss H. Martin, visiting from the University of Adelaide, is examining Tertiary and post-glacial microfossil successions.

The Institute of Oceanography is undertaking a study of foraminiferal faunas and sediments from the inlets and straits along the British Columbia coast. A. E. Cockbain is completing an examination of the distribution of foraminifera in the Juan de Fuca, Georgia, and Queen Charlotte Straits.

In the Geology Department, R. Best and graduate students M. Williams and Miss R. Smith are investigating growth stages of the ostracods *Kloedenella* and *Dizygopleura*. Three graduate students are investigating Foraminifera. D. Scott is working on the late Paleozoic Rocky Mountain formation of the southern Canadian Rockies, R. Yole on the paleontology and stratigraphy of early Pennsylvanian limestones near Cowichan and Horn Lakes, Vancouver Island, and C. Smith on stratigraphy and paleontology of Pennsylvanian rocks of northwestern Washington.

H. Trettin has collected fusulinids, including *Conodofusiella*, *Schwagerina*, and *Yabeina*, from Permian rocks of the Cache Creek group north of Lillooet, British Columbia.

W. R. Danner is continuing work on the poorly known Paleozoic limestones of southwestern British Columbia. *Paramillerella*, *Ozawainella*, *Plectogyra* and *Tetrataxis* have been obtained from Pennsylvanian beds, and *Fusulinella* from one sequence on Vancouver Island. Lower Permian limestones have yielded *Pseudofusulinella* and *Schwagerina*, while Middle to Upper Permian beds contain different species of *Schwagerina*, along with *Dunbarula*, *Neoschwagerina*, *Pachyphloia*, *Verbeekina* and *Yabeina*. He also reports Upper Cretaceous foraminifera from limy sediments interbedded with pillow lavas on the south side of Lopez Island, San Juan Islands, Washington. These rocks were previously regarded as Paleozoic in age. Eocene foraminifera have been collected from the east side of the Olympic Peninsula, Washington. R. Cox has obtained spores, pollen and invertebrates from the Sooke sediments of Vancouver Island that should assist in dating these deposits.

McMASTER UNIVERSITY (HAMILTON)

Muskeg studies continue to be an important subject, under the direction of N. W. Radforth. These studies are concerned with concepts of deposition and accumulation of vegetation, and differential fossilization. Three Ph. D. studies in micropaleobotany are in progress. Miss Lynda Suguitan is engaged in a comparative study of spores and pollen in peat from largely unconfined organic terrain. The extent to which the top several inches can be regarded as reflecting the history of deposition and consistency of contemporary surface cover is being assessed. The distribution of *Juniperus communis* pollen is also under study. J. Stewart is assessing the significance of cuticles in peat as a means of interpreting the origin and evolution of vegetal composition. R. Eydt is evaluating fossilized tissues in peats as a means of comparing different kinds of peat.

Plant remains have been found in preparations of Silurian rocks from Ontario. Micropaleobotanical work is continuing on the Carboniferous Minto beds of New Brunswick and the Devonian Sextant formation. Papers in preparation by N. W. Radforth include: "An assessment of the component tissues of peat in their *in situ* arrangement", and "Cuticle in organic terrain as applied to Capetown Bog."

UNIVERSITY OF SASKATCHEWAN (SASKATOON)

Dr. Margaret W. Steeves reports two projects. The first is a palynological analysis of the Lower Cretaceous Blairmore formation in Saskatchewan. In cooperation with the Institute for Northern Studies, analyses are being made of Pleistocene deposits in northern Saskatchewan and adjacent areas.

MICROPALEONTOLOGICAL CONSULTANT

A. McGugan of Calgary is continuing work on Upper Cretaceous foraminifera of Vancouver Island, and will report on this project at the Denver A.A.P.G. meetings. Comparative material from California is needed, particularly from Goudkoff's foraminiferal zones, especially *Bulimina petroleana* (P. O. Box 672, Calgary, Alberta). He will also report on Permo-Carboniferous stratigraphy of the Banff area, Alberta, at Denver.

THE CALIFORNIA STANDARD COMPANY (CALGARY)

Huon Walton has started a palynological laboratory. Miss Pauline Ness of the University of Alberta is his assistant.

IMPERIAL OIL LIMITED (CALGARY)

J. Jansonius has completed his investigation of microfloral assemblages of Permian and Triassic age in Alberta and British Columbia. With S. A. Pocock, he will prepare a paper on the palynology of the Permian Hilton Plant Beds, Westmorland, England. S. A. Pocock has completed a palynological study of the Jurassic-Cretaceous boundary in Canada and Europe. Notes on the type of *Cingulatisporites* and on Cretaceous species of *Murospora* (in press, Jour. Paleontology) have been prepared. With C. H. Crickmay, he is continuing work on the Cretaceous-Eocene boundary of the Vancouver area. F. L. Staplin has revised his "Pleistocene Freshwater Ostracoda of Illinois," and

will soon submit it for publication. The work was done with the aid of the Geological Survey of Illinois and the University of Illinois. His paper entitled "Reef-controlled distribution of Devonian microplankton" will appear in Palaeontology, vol. 4, no. 3. Some 40 species of hystrichospherids are described, a number of genera are revised, and new structures in Chitinozoa are illustrated. A note on *Torispora*-like spores (Famennian, Tournaisian) has been submitted for publication.

P. C. McGill is working on ostracodes of the Beaverhill Lake formation (Devonian, Taghanician age) of Alberta, especially those of the *Ropolonellus-Plagionephrodes* group. He is anxious to exchange material and correspond with other workers studying the same genera (Imperial Oil Limited, 339–50 Ave. S.E., Calgary, Canada).

SHELL OIL COMPANY OF CANADA LTD. (EDMONTON)

General micropaleontology is under the direction of T. P. Chamney. Investigations in this field in western Canada started in 1953. Wherever possible, interpretations are checked against macropaleontological, time-stratigraphic control. The regional framework and numerous detailed studies have been completed from the United States border to the Arctic. Paleozoic non-fusulinid foraminifera are being assessed for use in correlation and possible chronological subdivision. Serial sections and organic thin sections are being used where disintegration processes are impossible. Solvent and mechanical means of carbonate rock disintegration have been the subjects of considerable research.

The work, under A. P. Audretsch, of setting up control assemblages, laboratory and staff for palynology is still incomplete.

Work on ostracodes started in 1958, with emphasis on Paleozoic rocks in general. It is presently under the direction of W. Braun.

MOBIL OIL OF CANADA LIMITED (CALGARY)

N. P. Elphinstone is interested in exchanging palynological slides or samples of Cretaceous, Jurassic, Mississippian and Devonian age from Western Canada for comparative material from Western Canada, Eastern Canada, or northeastern United States (Mobil Oil Bldg., Calgary, Canada).

TEXACO (CANADA) LIMITED (CALGARY)

K. O. Parsch has extended his studies of the Paleozoic microfaunas (especially Devonian and Mississippian ostracods) and is also studying stratigraphic and environmental problems in the Mesozoic rocks of Alberta and the Northwest Territories. He has completed a Canadian micropaleontological bibliography for the period 1785–1957.

FRANK L. STAPLIN
Imperial Oil Limited
Calgary, Alberta, Canada

JAPAN

K. ASANO

Progress in micropaleontological studies in Japan since the last news report appeared in January, 1960, is reviewed in this report.

TOHOKU UNIVERTITY

A Memorial Volume dedicated to Dr. Shoshiro Hanzawa upon the occasion of his retirement in March 1960 was published in Science Reports of the Tohoku University, Second Series, Geology. It contains many papers on foraminifera, including the works of Drs. Orville L. Bandy, W. Storrs Cole, Irene Crespin, M. F. Glaessner, George L. Harrington, Inge Küpper, Frances L. Parker, Fred B. Phleger, Ruth Todd, M. L. Thompson, Kiyoshi Asano, Michihiro Kawano, Yoshiro Tai, Shigeo Murata, Yokichi Takayanagi, Hisayoshi Igo and Nobuhiro Hatae. Dr. Hanzawa was appointed Professor Emeritus of the Tohoku University in recognition of his work in micropaleontology.

Dr. Hanzawa is continuing his studies on larger foraminifera and his work "The Upper Cretaceous and Tertiary Three-layered Larger Foraminifera and their allied Forms" will be published in MICROPALEONTOLOGY early in 1962.

Dr. Kotora Hatai has been appointed successor to Dr. Hanzawa as Professor of Historical Geology.

In the regular series of the Science Reports (vol. 32, no. 1), Dr. Y. Takayanagi published a monographic work on the "Cretaceous Foraminifera of Hokkaido, Japan," and his work on Cretaceous foraminifera is continuing.

In 1959, Dr. K. Asano collected Danian type planktonic foraminifera from the Cretaceous formations near Nemuro in Hokkaido to be used in a joint study with Dr. Alfred R. Loeblich, Jr. Planktonic Foraminifera were found in abundance in the Paleogene formations of Kyushu, and these were determined to form a zonal sequence from Eocene to Miocene. The results will be published shortly. Dr. Asano is also studying the foraminifera collected from the Miocene globigerinid limestone of one of the Emperor seamounts in the North Pacific.

Mr. T. Saito has made a micro-biostratigraphic study of the Tertiary System of the Kakegawa District, Shizuoka Prefecture, and a part of the results have been published in Contributions from the Institute of Geology and Paleontology, Tohoku University (1960). He finds that the globigerinid from the Miocene formations of Japan can be used in world-wide correlation.

Dr. K. Sohma has been studying the pollen floras from the Tertiary and Pleistocene of various parts of the Japanese Islands and a part of his results have already been published. He will leave for America shortly.

TOKYO UNIVERSITY

On the occasion of the Twenty-fifth Anniversary of the Paleontological Society of Japan, held in January 1961 at the Tokyo University, Dr. Hisakatsu Yabe, Honorary President of the Society was awarded the Society Medal in recognition of his works, and Drs. Tetsuro Hanai, Taro Kanaya, Tamio Kotaka and Tsugio Shuto were presened with the Society Award of a Diploma and Research Fund in recognition of their work. The "Catalogue of Type specimens of Fossils in Japan," compiled by Drs. S. Hanzawa, K. Asano and F. Takai, was published as a project of the Twenty-fifth Anniversary of the Paleontological Society of Japan. This includes a total of 5,856 species distributed throughout the Animal and Plant Kingdoms.

Dr. T. Hanai has already published his "Studies on the Ostracoda from Japan, 1–V and Historial Review" in the Journal of the Faculty of Science, University of Tokyo, and his work on the Ostracoda is being pursued.

An account of Dr. T. Uchio's project at the Scripps Institution has already been published in the Cushman Foundation for Foraminiferal Research, Spec. Publ., No. 5, 1960, under the title of "Ecology of Living Benthonic Foraminifera from San Diego, California." He is now making similar studies on the Recent foraminifera from the seas surrounding Japan.

TOKYO UNIVERSITY OF EDUCATION

Dr. H. Ujiie and Mr. K. Oshima made a joint statistical study of the Japanese miogypsinids, and the first report was published in Science Reports of the Tokyo Kyoiku Daigaku, Sec. C, no. 62. In no. 63 of the same Journal, Dr. H. Ujiie and Mr. H. Watanabe published on the Poronai foraminifera from Hokkaido.

Dr. H. Igo has started a monographic study on the Fusulininae of Japan, and Mr. A. Ishii is working on the Ozawainellinae and Staffellinae.

Dr. H. Fujimoto retired from the Tokyo University of Education in 1959 where he held the chair in Historical Geology and Paleontology. He is now Professor of Geology in the Yamagata University, and is continuing his studies on the Paleozoic stratigraphy and paleontology of the Hida Massif.

SAITAMA UNIVERSITY

Dr. R. Endo, who has been studying the Paleozoic calcareous algae of Japan, retired in August 1960. A Memorial Volume is being planned for him.

Dr. R. Morikawa is an active worker on the fusulinids of Japan. In 1960 he published three papers on the fusulinids in the Science Reports of the Saitama University. Presently, he is working on a monograph of the Japanese Schwagerininae, in collaboration with Mr. Y. Takaoka.

KYUSHU UNIVERSITY

Since June 1960, Dr. M. L. Thompson has been visiting Kyushu University as a Fulbright Professor. He expects to return home in January 1961. Besides teaching at Kyushu University, he has also lectured on the fusulinids at Tokyo University, Tohoku University, Hokkaido University and Kanazawa University.

After the publication of monographic work on the fusulinids of the Akiyoshi limestone, Dr. R. Toriyama is continuing his studies on the fusulinids. Together with Mr. T. Sugi, he has published a paper on the Permian fusulinids of Thailand in the Memoirs of the Faculty of Science, Kyushu University, vol. 9, no. 1.

Dr. K. Takahashi has been, and still is, studying the pollen flora from the coal-fields of Kyushu and his recent paper "Vorläufige Mitteilung über das Problem der Oostuji und Ashiya-stufe des Alttertiärs von Kyushu" was published in Memoirs of the Faculty of Science, Kyushu University, vol. 9, no. 3.

HOKKAIDO UNIVERSITY

In 1959, Dr. S. Honjo published two papers, "Neoschwagerinids from the Akasaka Limestone" and "The axial septula of some Japanese Neoschwagerininae", in the Journal of the Faculty of Science, Hokkaido University, ser. 4, vol. 10, nos. 1, 2. He is, at present, at Princeton University where his studies on the fusulinids are continuing.

Dr. T. Shirai, as a result of his studies on the Pliocene foraminifera from the Setana formation, described a new genus which he named *Discotruncana*. This paper was published in the Journal of the Faculty of Science, Hokkaido University, vol. 10, no. 3.

KANAZAWA UNIVERSITY

Dr. W. Ichikawa published "On the Fossil Marine Diatoms in the Wakura Beds, Noto Peninsula, Japan" in the Science Reports of the Kanazawa University, vol. 7, no. 1. He is pursuing his studies on the Tertiary diatom flora of Japan.

Mr. N. Fuji's recent paper "The Palynological Study of Cenozoic Strata, Hokuriku Region, Central Japan, lst Rep.–On Alluvial Peat from Ishikawa and Fukui Prefectures", was published in the Science Reports of the Kanazawa University, vol. 7, no. 1. He is now working on the value of pollen in micro-stratigraphy.

KIYOSHI ASANO
Institute of Geology and Paleontology
Tohoku University
Sendai, Japan

PERU

RAYMOND E. MALLOY

This is the first report of your new correspondent who, in addition to becoming acquainted with Tertiary faunas and biostratigraphy of northwestern Peru, has been busy establishing Peru's first full-time palynological laboratory.

The center of micropaleontological activity for Peru continues to be in the northwestern sector of the country, where there is a total of eight micropaleontologists, all engaged in petroleum exploration and development studies.

EMPRESA PETROLERA FISCAL (EPF)

The EPF paleontological laboratory is presently concerned primarily with routine well work. Mr. Federico Seminario, head of the laboratory, has acquired an assistant, Mr. Tomas Valdespino H., whom he is now training in the use of foraminifera for routine subsurface correlation.

Plans to carry on palynological studies at EPF have been postponed until Mr. Seminario receives university training in this field, outside Peru.

INTERNATIONAL PETROLEUM COMPANY, LTD. (IPC)

The work of the Talara Paleontological Laboratory is divided more or less equally between routine paleontological determinations for drilling wells and biostratigraphic studies of a regional nature.

Studies of the latter type for International's Joint Interest properties to the north of La Brea-Pariñas have been carried out in the past year. No major lateral changes in foraminiferal facies appear to have occurrred in the Eocene and Paleocene basins there, but the structural complexity is great.

Another phase of the laboratory's work, the study of surface samples from the Montaña of eastern Perú, has demonstrated the value of the charophytes and ostracodes in zoning the Tertiary and uppermost Cretaceous sediments there. Mr. Fernando Zúñiga is doing this work, with the assistance of Mr. Elías Aliaga.

The palynological laboratory has been in full-scale operation since December 1960, and satisfactory progress in recovering and studying assemblages of spores, pollen, hystrichospherids, and dinoflagellates characteristic of the marine Eocene and Paleocene beds here is being made.

The laboratory staff has undergone some changes since the writer assumed his duties as section head. Mr. C. L. Wilmott transferred to the Pool Studies Section of the Geology Department early in 1960, and later left Talara in December to take up residence in the United States.

Two experienced micropaleontologists were added to the staff in 1960. Mr. Alejandro Euribe joined us after several years with Mene Grande Company in Venezuela. He is a graduate of San Marcos University in Lima and received a Master of Science Degree in Geology from Stanford University, California. Mr. José Cruzado, also a graduate of the University of San Marcos, joined our group after two years with the Peruvian Mission of the United States Geological Survey.

Mr. J. A. McCormick, who now has been more than three years in the laboratory, is carrying out regional biostratigraphic studies for International's Joint Interest properties of Lobitos and El Alto.

Your correspondent is presently engaged in the training of Mr. Euribe in the theoretical and practical aspects of palynology and also, instructing the laboratory technician with sample processing.

PERUVIAN PACIFIC PETROLEUM COMPANY

Paleontological studies of both an exploratory and routine nature are under way at the Peruvian Pacific laboratory in Negritos. Mr. Wayne Elliot is in charge of the work and has studied a large number of auger hole samples from mapped surface formations, for their arenaceous and calcareous foraminiferal faunas. The semi-routine study of samples from offshore wells has revealed some interesting paleontologic and stratigraphic problems. Mr. W. T. Rothwell has returned to the Richfield offices in the United States.

CERRO DE PASCO CORPORATION

Cerro de Pasco is at present the only company operating outside of northwestern Perú which retains a paleontologist, Miss Rosalvina Rivera, in connection with their exploration in the Montaña. Miss Rivera is concentrating her effort on the Charophyceae, useful in zonation of Tertiary and Upper Cretaceous beds of eastern Perú where these microfossils are found in rocks which often contain no other microfossils of any sort.

OTHER NEWS

Geologists, paleontologists (among them your correspondent) and mining engineers from oil and mining companies, as well as from Perú's several universities, were on hand in Lima during the week of December 12, 1960, for the Second National Peruvian Geological Congress.

Attendance at the technical sessions was very good and, judging by questions from the floor, there is a lively interest in all phases of geological work in Peru.

The technical program, consisting of 30 papers presented by members of the Peruvian Geological Society and guests, covered a broad range of topics, including hydrology, geomorphology, sedimentology, paleoclimatology, mineralogy and petrology, paleontology, structural geology, and seismology. Space limitations prevent any detailed discussion of individual papers here, but those of interest paleontologically should be mentioned.

Miss Rosalvina Rivera gave a brief presentation of her work on the Charophyceae entitled "*Species of Chara from the Cretaceous-Tertiary Sequence of Eastern Peru*" in which she described the occurrences of seven species of the genus *Chara* in Upper Cretaceous, Paleocene and Eocene rocks of Peru, east of the Andes.

Your correspondent, gave a paper entitled "*The Stratigraphic Application of Palynology in Peru*". The topics discussed were a general introduction and definition of palynology and, following, an outline of the work done by the writer and Mr. R. B. Hulsman (formerly of International Petroleum Co., Bogotá, Colombia) in defining acid-insoluble microfossil species from Tertiary and Cretaceous rocks of Peru.

Other paleontological papers, given by title or abstract, were the following: "*New Genera and Species of Lower Cenozoic Otoliths Allied to Myripristis (Pisces, Beryciformes, Holocentridae)*" by Don L. Frizzell and C. Kurt Lamber of the Missouri School of Mines and Metallurgy, and "*The Occurrence of Nonion stainforthi in Northwest Peru and Other Localities*" by José Cruzado of the International Petroleum Company's laboratory at Talara.

RAYMOND E. MALLOY
International Petroleum Company, Ltd.
Talara, Peru

SPAIN

GUILLERMO COLOM

The search for oil in Spain continues at an increasing tempo and is giving rise to an unparallelled amount of micropaleontological study of this country's territory.

Andalusia, the Ebro basin, and the northern provinces of the Peninsula are being explored for petroleum, and also the Spanish Sahara. In general, the micropaleontological laboratories connected with the various companies, most of which are foreign, are established abroad.

H. J. Oertli has an interesting paper in the Revue de Micropaléontologie, no. 3, 1960, on the evolution of an ostracod from the Lutetian of the province of Huesca (Catalonia) in the Spanish Pyrenees. He shows the changes in ornamentation seen in a species of *Echinocytheries*, from a pustulous test at the beginning, to a reticular arrangement in its later forms. A precise knowledge of the evolution of the ecological medium can explain these gradual changes, which are always of interest in local stratigraphic geology.

A number of recent papers on the geological structure of the Betic mountains in southern Spain give useful micropaleontological data for the determination of the Secondary and Tertiary formations of this very difficult region.

Foraminifera, ostracoda, tintinnids, globochaetas, stomiosphaera etc. help define the lithofacies with greater precision. R. Busnardo and M. Durand Delga (Données nouvelles sur le Jurassique et le Crétacé inférieur dans l'Est des Cordillères bétiques) have written on the region of Alicante; M. Durand Delga and J. Magné on the Tertiary (Une coupe du Tertiaire prébétique de Benitachell). A. Foucault has worked on the Nummulitique of the region of Granada (Sur la tectonique de la zone subbétique de la région de Huescar et sur son Nummulitique). Miss A. Linares has listed microforaminifera from the Upper Eocene, including *Sporohantkenina bermudezi* and *H. suprasuturalis* (Données micropaléontologiques sur les environs de Domingo-Perez (chaine subbetique).

Further south, in the province of Cadiz, P. Chauve has described interesting micropaleontological associations, from the neritic Lias with *Coskinolinopsis*, to the levels of the Tithonian and Berriasian filled with tintinnids (Etude de quelques affleurements jurassiques de la région d'Alcalá de los Gazules). J. Didon has another paper on the same region relating to the arenaceous flysch of upper Oligocene to the Miocene age, with *Miogypsina* and *Miogypsinoides*. Certain tectonic unities carry Secondary formations with fine bathyal limestones containing *Nannoconus* and Lower Cretaceous tintinnids.

All of these papers appeared in the Bulletin de la Société Géologique de France, vol. 2, no. 3, 1960 and are interesting aids in deciphering the complicated tectonics of the Sierras Beticas.

GUILLERMO COLOM
Soller, Majorca
Spain

UNITED STATES

EAST-CENTRAL REGION

ROBERT V. KESLING

UNIVERSITY OF NOTRE DAME

Dr. R. C. Gutschick is specializing in early Mississippian microfaunas. His preliminary studies on arenaceous foraminifera of the Welden limestone of Oklahoma, Chappel limestone of Texas, Lodgepole limestone, and Sappington sandstone of southwestern Montana are completed and manuscripts submitted for publication. Dr. Gutschick is now working on a holothurian sclerite and conodont fauna from the basal Lodgepole, and a microfacies-faunal study of the Sappington and Lodgepole formations. He published "Early Mississippian (Lower Carboniferous-Tournasian) Micropaleontology in the United States," (XXI Int. Geol. Congress, pt. VI, p. 114–34, 1960).

Dr. E. M. Winkler is continuing his work on Pleistocene freshwater ostracodes. He published "Post-Pleistocene ostracodes of Lake Nipissing Age", (Jour. Pal., vol. 34, no. 5, pp. 923–32, 1960), and has submitted to that journal a paper on "Two Late Pleistocene (Cary) Freshwater ostracode faunas."

UNIVERSITY OF LOUISVILLE

Dr. James Conkin has completed his monograph on the "Mississippian Smaller Foraminifera of southern Indiana, Kentucky, northern Tennessee, and south-central Ohio". This work will be published in the Bulletin of American Paleontology in 1961. At present, he is completing a paper describing the foraminiferal fauna of the Louisiana limestone of Missouri and southwestern Illinois.

UNIVERSITY OF WISCONSIN

Prof. Roger Batten has brought us up to date on micropaleontology at Wisconsin. Five years ago he joined the staff and revived the micropaleontology course that had been given by Dr. M. L. Thompson up to 1952.

Thus far three Master's theses have been completed. James I. Jones undertook a statistical study of *Praeglobotruncana gautierensis ("Globigerina cretacea")* from the Eagle Ford group in Texas, (Contributions from the Cushman Foundation, vol. 11, no. 212, July, 1960). Margaret Johansson completed an analysis of variance study of conodont distribution and association of genera in the Lake Neosho shale (Desmoinesian) of Iowa, Missouri, and Kansas. Donald Barness investigated the guembelinids of the upper Taylor Formation in Texas and statistically studied their distribution and their planktonic nature. Both of these studies are unpublished Master's theses for 1960 at the University of Wisconsin.

Two active ecological investigations of recent Foraminifera are under way. James I. Jones, is doing a study of the ecology of living planktonic foraminifera of the Caribbean Basin and the Tongue of the Ocean. Thus far he has over 350 samples of plankton accurately collected with temperature and complete water analyses of each station. The program is being supported by the Wisconsin Alumni Research Foundation and the University of Miami, Marine Laboratory. At this writing, Jones is on a cruise off Panama with the Scripps research vessel *Beard*, filling in gaps in the Caribbean sampling. This ecological project will continue for several years (it was initiated in the summer of 1958), and a portion of the study will be used for a Ph. D. dissertation.

The second study is concentrated in Florida Bay and along the entire length of the Florida Keys. It is a study of the ecology and distribution of benthonic Foraminifera. We have been actively collecting this area for three years and hope to keep studies going indefinitely as a source for theses. Currently, George Lynts is doing a preliminary distribution analysis of the northern Bay area and Sally Scholz the southern Bay area for Master's theses. Wayne Bock is completing a taxonomic study of the benthonics of the central Bay region.

MIAMI UNIVERSITY, (OHIO)

Dr. John K. Pope is now the micropaleontologist at Miami, succeeding Dr. K. E. Limper, who became Dean

of the College of Arts and Science. Dr. Pope writes, "A master's student here, Roland Grygo, is currently working on the scolecodonts of the Arnheim and Waynesville formations of the Richmond. Arnheim pickings are poor, Waynesville good, and if anyone is interested, the Liberty is loaded. Another master's student, Richard Thompson, is wrestling with Waynesville bryozoa, if these, by merit of his stacks of thin sections, fall into the realm of micropaleontology. John Duffy, a third master's student, is doing background work for an ostracod thesis, either the Southgate or Waynesville. The Waynesville is so popular here because it is so fossiliferous and because Bull Run, with its superb section, virtually flows through our building."

UNIVERSITY OF ILLINOIS

Dr. William Hay has joined the staff of the Geology Department, and will teach invertebrate paleontology and paleoecology. His special interests are foraminifera, discoasters, and ostracodes. Dr. Harold W. Scott states, "As for myself, I have three current projects. Mr. Albert Guber is in the middle of a study on Late Ordovician ostracodes from the Cincinnati area. Mr. Robert Lundin and I have a study on *Phannasymetrica* nearly completed. Miss Betty Hanagan has just started a Ph. D. thesis project on Middle Ordovician ostracodes, and Mr. McGuire is in the early stages of a paleoecological and phylogenetic study of Pennsylvanian conodonts."

UNIVERSITY OF MICHIGAN

Your correspondent and his students have spent some time on extracting ostracodes from the Bony Falls limestone, which they have correlated with the Black River of the Midwest by the occurrence of *Eoleperditia fabulites*. Specimens are difficult to exhume, but are well preserved. Three parts of the study have been published in the Contributions from the Museum of Paleontology. One concerned the discovery of dimorphism in *Macronotella scofieldi*, altering the current concept of the affinities of this genus. Another described several species of *Platybolbina* with distinctive ornamentation. Other ostracodes from this diverse fauna are being investigated.

OHIO STATE UNIVERSITY

Within the past year, Mr. Dick Pulse and Dr. Walter C. Sweet completed and published (in the Journal of Paleontology) a study of conodont-elements from the Fairview and McMillan formations of Ohio, Indiana, and Kentucky. Their lab is now busy reducing some two tons of bulk material collected from a dozen sections through the sub-Eden Cynthiana formation of Ohio and Kentucky. Residues are yielding thousands of conodonts and they hope for the same success in zonation achieved in studies of the Eden, Fairview, and McMillan.

Early this year, Mr. Stig M. Bergström and Dr. Sweet completed a study of a large collection of conodont-elements from the Middle Ordovician Pratt Ferry formation of Alabama. The fauna is of particular interest for it is European in aspect and affords a type of precise correlation with the now rather well-known Scandinavian section not heretofore possible. Furthermore, this is the first conodont fauna of any significance reported from the entire Appalachian province!

Mr. James Scatterday is now in his second year of study of microfossils, particularly conodont-elements, ostracodes, and endothyrids, from the late Mississippian Maxville limestone of Ohio. Frequencies are low and he is "running" very large samples in order to obtain satisfactory collections.

Prof. Summerson has in mind, perhaps has already begun, a study of Silurian arenaceous Foraminifera from Illinois. Mr. Joseph Schwietering is working with Foraminifera and Ostracoda from late Cretaceous strata in central Utah, and Mr. Claude Rust and Mr. Roger Williams are studying the distribution of microfossils, particularly conodonts, in well cuttings and cores from western and southwestern Ohio. Mrs. Anita Epstein is continuing a study of a rich collection of ostracodes from the Port Ewen limes one of New York.

ROBERT V. KESLING
University of Michigan
Ann Arbor, Michigan

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Comments and Errata

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On page 105, the correct magnifications for *Lockhartia susuaensis* are: Plate 4, fig. 1, × 55; fig. 2, × 53; figs. 3–4, × 53, fig. 5, × 53 and fig. 6, × 53.

JENKINS, D. GRAHAM

Planktonic foraminifera from the Lakes Entrance oil shaft, Victoria, Australia. Micropaleontology, vol. 6, no. 4, pp. 345–371, pls. 1–5, text-figs. 1–10, October, 1960.

On page 357, for *Globorotalia glomerosa* (Blow) subsp. *glomerosa* (Blow) read *Candorbulina glomerosa* (Blow) subsp. *glomerosa* (Blow).

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